# AN INTRODUCTION TO
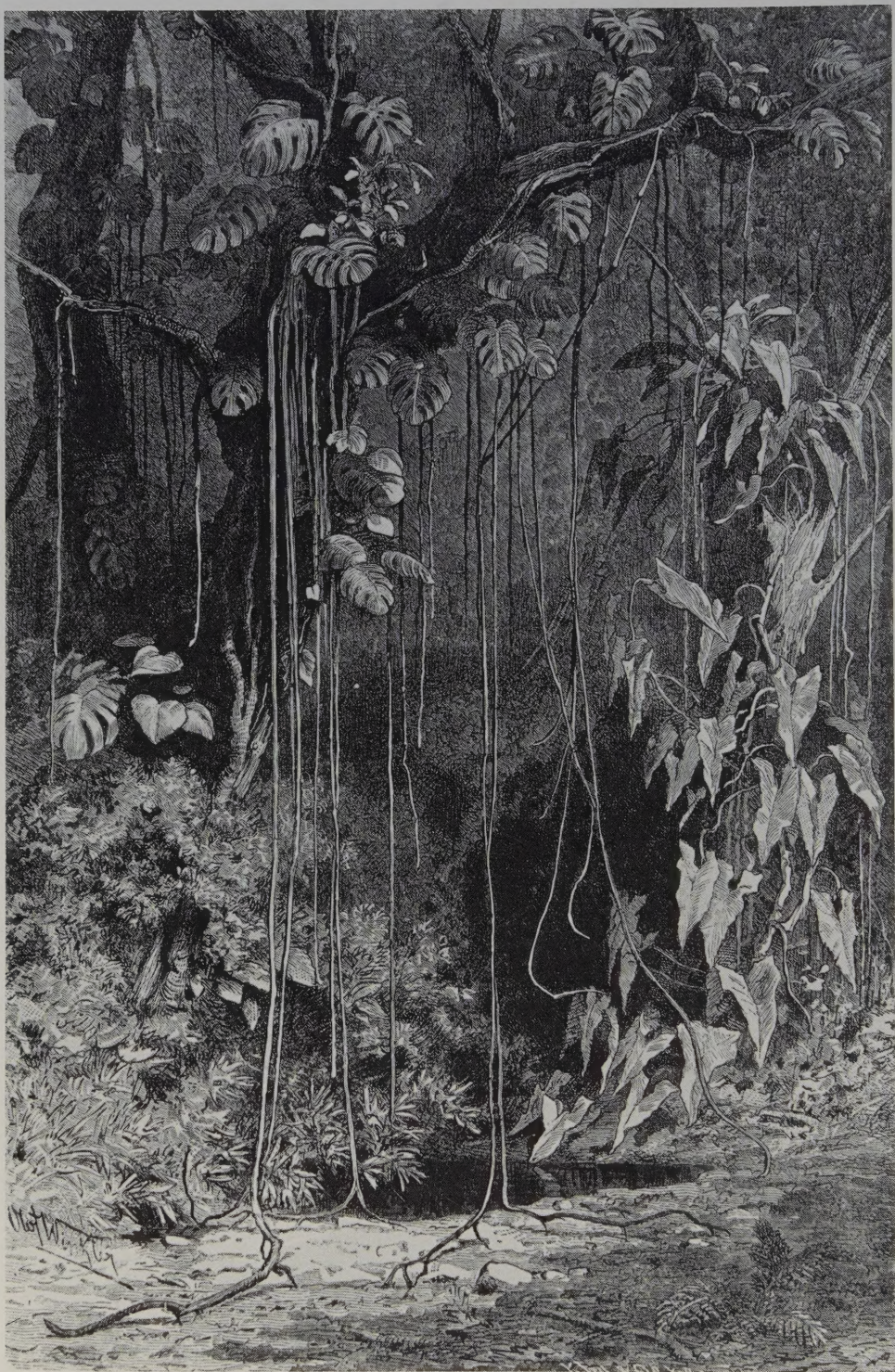
# TROPICAL RAIN FORESTS

## T. C. WHITMORE

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*T. C. Whitmore*

# Preface

The aim of this book is to provide an introduction to the world's tropical rain forests for a broad audience, to describe their structure and functioning, their value to man, and what he is doing to them. Examples are drawn from all parts of the humid tropics. Today there is more research being conducted in tropical rain forests than ever before. Some is driven by curiosity, some by the desire to harness these forests to mankind's needs. What generalizations can be made? To what extent are there real differences between rain forests in different places, and what are the current frontiers of knowledge? Is present-day concern about man's impacts on tropical rain forests justified? The book seeks to provide an answer to these questions, at a simple level accessible to all who want to know something about these grand forests.[†]

In lands where tropical rain forests occur man has lived in closest dependence on them since time immemorial. Europeans became aware of them over two millenia ago (Chapter 1). Increasing knowledge since the Renaissance with the voyages of discovery and then the colonial era revealed that there are in fact many different kinds of tropical rain forest (Chapter 2). Plants exist in a luxuriance and a diversity of bizarre forms undreamed of in temperate latitudes (Chapter 3). Animal life is also rich and diverse (Chapter 4). Modern science continues to unravel the many kinds of complicated interdependence of plants and animals, for example in flower pollination and seed dispersal (Chapter 5). Tropical rain forests have waxed and waned in extent through geological time, and the present patterns of species' distributions are a result of these historical events. The former idea that these great forests have survived immutable 'since the dawn of time' is a romantic fallacy, as investigations of the last three decades have shown (Chapter 6). The forests are also continuously changing at the other end of the time scale, the life span of an individual tree. The elucidation of forest dynamics (Chapter 7) has been the other major breakthrough of recent years. We now know a great deal about the ecology of individual tree species and the particular requirements for growth of their seedlings in canopy gaps formed by the death of big trees. Silviculture, the manipulation of forests by man to favour tree species of his choice, is dependent on understanding these innate characteristics. Tropical rain forests can be a sustained source of timber, renewed by regrowth after felling, so long as (and it is a vital proviso) man works within the limits of their natural dynamics. Tropical rain forest nutrient cycles (Chapter 8) are also now reasonably well understood, with enough detailed studies made for tentative generalizations to be possible. The old ideas of a closed cycle and with nearly all the nutrients in the plants have not survived. Shifting agriculture is now well-known to be a sustainable form of farming, suitable for infertile soils. Sustainable human utilization of forest lands for crops or trees depends, as with silviculture, on working within the natural limits of the nutrient cycle.

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[†]To aid comprehension some of the more technical or specialized terms are defined in a glossary at the end of the book, and some concepts are discussed more fully in the text notes

One of the driving forces of science is the puzzles found in nature. Of these one of the greatest is to understand the phenomenal species richness of tropical rain forests. The extremes so far discovered are a $100 \text{ m}^2$ plot in Costa Rica on which grew 233 species of vascular plants (including 73 tree species, mostly as seedlings) (Table 2.3), and a $1000 \text{ m}^2$ plot in Peru with 580 trees of over 10 cm in diameter, of which every second stem was a different species (Fig. 2.27). In both samples the study plot did not contain all the species in its locality. Many different factors already mentioned contribute to this hyper-richness; they are brought together in Chapter 9.

The book ends with a consideration of human impact on tropical rain forests, Chapter 10. This final chapter starts with a historical sketch of increasing intervention through historical time. Present-day impacts are described, and it is shown that pantropical generalizations are simplistic and misleading. The very real causes for concern are analysed. These have led to the increasing public unease, and this in turn has triggered a response in governments, international institutions, and businesses which, as this book goes to press, is suddenly accelerating. Because of this response, the book is able to end on an optimistic note. All is not yet lost of the world's tropical rain forests. There are still big gaps in our scientific understanding which need urgently to be addressed. But mankind has the ability to discover how these self-perpetuating dynamic ecosystems work and then turn that knowledge to advantage. The present book aims to review the scientific basis for good decisions. If human societies can then exercise the self-restraint to utilize rain forests by working within their natural limits the cries of doom and gloom of the late 'eighties will have served a useful purpose. This is a big 'if'.

Why have tropical rain forests always been so thrilling to biologists? What is their excitement that drives scientists throughout the world forward when for most the pay is so poor and the support of their employing institutes and universities minimal? Is present public concern about rain forests justified? Are they really disappearing, and if they are, does it matter? Are they so fragile that their sustainable utilization is impossible? These are the questions to which the following pages are addressed.

*Witney, Oxon*
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T.C.W.

# Acknowledgements

# An Introduction to Tropical Rain Forests

*By the same author*

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# Contents

# Note on references and further reading

This book is an introduction to tropical rain forests and the text aims to discuss the main topics. The reader who wants to discover more can do so via the notes at the back of the book which are referred to by superscript numbers in the text. In the text notes are named original research papers on which particular points are based. In addition, for every Chapter these text notes include a selection of books and review papers which give fuller information than there is space for here. The sources of data included in Figures and Tables are given in their captions. All the papers referred to in text notes, Figures, and Tables are cited together at the end of the book.

Knowledge of tropical rain forest fills a great warehouse. The references cited have been carefully chosen to help the reader peer through its windows and discover the huge store of knowledge arranged within its walls.

## Note on units, symbols, and abbreviations

Throughout this book SI units are used. The convention is followed that values such as metres per year or stems per hectare are shown as m year$^{-1}$, stems ha$^{-1}$ not m/year, stems/ha.

> means 'greater than'
≥ means 'equal to or greater than'
< means 'less than'
≤ means 'equal to or less than'

B.P. means years Before Present
$c.$ = circa, about
M = mega, $10^6$
n = nano, $10^{-9}$
s.l. means 'in the broad sense'

# 1

# An introduction to tropical rain forests

Rain forests have crossed a threshold of perception. No week passes without a new report on television, radio, or in the press of another piece of destruction, or a new message of gloom for the planet.[1] The public is left in no doubt that something nasty is happening down on the Equator. Man's present-day impact on tropical rain forests is, however, just the last stanza of a saga stretching back into the past beyond the beginning of written history.

European knowledge of tropical forests began when Alexander the Great crossed the Khyber Pass in 327 BC, into the Punjab, to establish the eastern limits of his short-lived empire on the banks of the Indus.[2] 'His army saw mangrove swamps (which upset conventional views on trees), jackfruit, mangoes, bananas, cotton, and banyans—which upset everybody's views on what roots are supposed to do'.[3] These bizarre findings were incorporated in the *Enquiry into plants* of Theophrastus, philosopher and pupil of Plato and Aristotle, to become part of the general knowledge of plants, copied, corrupted, and not improved upon for nearly two thousand years until the great voyages of discovery of the sixteenth and seventeenth centuries and the subsequent European colonial expansion.

The word jungle, still often in use, comes from the Hindi jangal, a reference to the dense impenetrable forest and scrub around settlements.

Tall stories percolated back to Europe from the early visitors (Fig. 1.1). For example, in the East poisoned arrows were discovered to be tipped with the sap of the upas tree,[4] accounts of whose identity and preparation mingled fact and fable. Of this the great Dutch naturalist G. E. Rumpf wrote in 1750:

Under the tree itself no plant, shrub or grass grows— not only within its periphery but, even, not within a

stone's throw of it; the soil is sterile, dark and as if burned. Such poisonousness does the tree exhibit that from the infected air birds perching on the branches are stupefied and fall dead, and their feathers strew the soil. So caustic were the branches sent to me in a stout bamboo vessel that when the hand was placed on the vessel, a tingling was produced such as one feels on coming out of the cold into the warmth. Everything perishes which is affected by its exhalation, so that all animals avoid it, and birds seek not to fly over it. No man dare approach it unless his arms, legs and head be protected by clothes.[5]

Osbeck, on a voyage from Sweden to China, stopped in east Java and, on 20 January 1752, saw a tree with flowers on its trunk. Cauliflory is unknown in northern Europe. He believed he had found a leafless parasite, and called it *Melia parasitica* (Fig. 1.2) naively commenting:

A small herb of barely a finger's length growing on tree trunks. It is so rare that so far as is known no one ever saw it before.[6]

With Colonial penetration scientific specimens began to flood back to the museums of Europe. At first the plants were the weeds of open places, many of which have wide occurrence. Indeed, when Linnaeus made his great synthesis of the world's plants, the *Species plantarum* of 1753, he believed from this evidence that the tropics had a rather species-poor and uniform flora.

The tropics had a powerful influence on the development of biology in the nineteenth century. Biogeography and ecology are both founded on the journeys in South America of the German Alexander von Humboldt, in the Andes (where he recorded how vegetation changes with climate) and in the lowland rain forests of Venezuela. He travelled with the Frenchman Aimé Bonpland. They arrived at Cumana, Venezuela, on 16 July

Fig. 1.1.. Early European travellers brought back exaggerated tales about tropical rain forests. This engraving from *Flora Brasiliensis* of von Martius, 1840 (plate IX) is a scene in the Atlantic coast forest of Brazil.

Fig. 1.2. Flowers borne on the trunk of *Dysoxylum parasiticum*, something unknown in northern Europe. When the Swedish botanist Osbeck saw this species in Java he thought the flowers were a leafless parasite. Solomon Islands.



1799 and the effect of the tropical environment led von Humboldt to write home:

What trees! Coconut trees 50–60 feet high; *Poinciana pulcherrima*[7] with a foot high bouquet of magnificent bright red flowers; pisang and a host of trees with enormous leaves and scented flowers, as big as the palm of a hand, of which we knew nothing ... We rush around like the demented; in the first three days we were unable to classify anything; we pick up one object to throw it away for the next. Bonpland keeps telling me he will go mad if the wonders do not cease.

Perhaps even more important for the development of biology was the stimulus the tropical rain forest gave to the minds of Charles Darwin and of

Alfred Russel Wallace in their independent expositions of the theory of evolution by natural selection. Darwin, as a young man 22 years old, went as naturalist on the voyage of the *Beagle*, whose first tropical landfall was Salvador on the Atlantic coast of Brazil (Fig. 10.12). He went ashore on 29 February, Leap day, 1832 and has recorded:

Delight ... is a weak term to express the feelings of a naturalist who, for the first time, has wandered by himself in a Brazilian forest. The elegance of the grasses, the novelty of the parasitical plants, the beauty of the flowers, the glossy green of the foliage, but above all the general luxuriance of the vegetation, filled me with admiration.... The noise from the insects is so loud, that it may be heard even in a vessel anchored several hundred yards from the shore.... To a person fond of natural history, such a day as this brings with it a deeper pleasure than he can ever hope to experience again.

Wallace spent five years travelling in South America (1848–52) and then eight more (1854–62) in the Malay archipelago where he discovered the two distinct faunas of the region, epitomized by the boundary Wallace's Line named after him (Chapter 6). He too was impressed by the richness of the forests:

If the traveller notices a particular species and wishes to find more like it, he may often turn his eyes in vain in every direction. Trees of varied forms, dimensions and colours are around him, but he rarely sees any one of them repeated. Time after time he goes towards a tree which looks like the one he seeks, but a closer examination proves it to be distinct. He may at length, perhaps, meet with a second specimen half a mile off, or may fail altogether, till on another occasion he stumbles on one by accident.[8]

Richness in species was one of the vivid discoveries of these nineteenth century explorer naturalists. It is now believed that about half the world's species occur in tropical rain forests although they only occupy about seven per cent of the land area. Herbs familiar in Europe have woody relatives which gives a whole new dimension to taxonomy:

Nearly every natural order of plants has here *trees* among its representatives. Here are grasses (bamboos) of 40, 60, or more feet in height, sometimes growing erect, sometimes tangled in thorny thickets, through

which an elephant could not penetrate. Vervains[9] form spreading trees with digitate leaves like the horse-chestnut[10] Milkworts,[11] stout woody twiners ascending to the tops of the highest trees, and ornamenting them with festoons of fragrant flowers not their own. Instead of your periwinkles[12] we have here handsome trees exuding a milk which is sometimes salutiferous, at others a most deadly poison, and bearing fruits of corresponding qualities. Violets[13] of the size of apple trees. Daisies (or what might seem daisies) borne on trees like alders.[14]

Tropical rain forest is certainly very different from the vegetation of northern Europe familiar to these naturalists, and few were able to resist recording their impressions in lyrical prose, or to exaggerate (Fig. 1.3). In perhumid climates, on normal tropical soils and at its grandest, as in the western Malay archipelago, it is, to use von Humboldt's phrase, forest piled upon forest, the topmost trees 45 m or occasionally even taller (Figs. 1.4, 1.5, 1.6), often as solitary emergents which stand head and shoulders above a billowing continuous canopy, many shades of green. Within the canopy[15] there are trees of all different heights, which sometimes locally occur in layers or strata (pp. 25–6), with crowns of many shapes. Trunks are mostly slender with only a minority exceeding a metre in girth. The trunks may be buttressed (p. 50), and the bark variously sculptured and coloured (p. 50). But the forest is more than just a collection of trees, as has been vividly described by E. J. H. Corner:

On its canopy birds and butterflies sip nectar. On its branches orchids, aroids and parasitic mistletoes offer flowers to other birds and insects. Among them ferns creep, lichens encrust, and centipedes and scorpions lurk. In the rubble that falls among the epiphytic roots and stems, ants build nests and even earthworms and snails find homes. There is a minute munching of caterpillars and the silent sucking of plant bugs. On any of these things, plant or animal, a fungus may be growing. Through the branches spread spiders' webs. Frogs wait for insects, and a snake glides. There are nests of birds, bees and wasps. Along a limb pass wary monkeys, a halting squirrel, or a bear in search of honey; the shadow of an eagle startles them. Through dead snags fungus and beetle have attacked the wood. There are fungus brackets nibbled round the edge and bored by other beetles. A woodpecker taps. In a hole a hornbill broods. Where the main branches diverge, a strangling fig finds grip, a bushy epiphyte has temporary root, and hidden

**Fig. 1.3.** The orang-utan of Sumatra and Borneo is in fact docile and shy and even if provoked is more likely to flee than to attack. This, the frontispiece to A.R. Wallace's *Malaya Archipelago*, gave the European reader the thrill he was expecting.

sleeps a leopard. In deeper shade black termites have built earthy turrets and smothered the tips of a young creeper. Hanging from the limbs are cables of lianes which have hoisted themselves through the undergrowth and are suspended by their grapnels. On their swinging stems grows an epiphytic ginger whose red seeds a bird is pecking. Where rain trickles down the trunk filmy ferns, mosses and slender green algae maintain their delicate lives. Round the base are fragments of bark and coils of old lianes, on which other ferns are growing. Between the buttress-roots a tortoise is eating toadstools. An elephant has rubbed the bark and, in its deepened footmarks tadpoles, mosquito larvae and threadworms swim. Pigs squeal and drum in search of fallen fruit, seeds and truffles. In the humus and undersoil, insects, fungi and bacteria and all sorts of animalculae participate with the tree roots in decomposing everything that dies.[16]

During the twentieth century knowledge of tropical rain forests developed in two streams.[17] On the one hand academic scientists continued to collect and identify the plants and animals, and to describe forest structure. Many of these studies were made on short visits of a few months' duration. They tried to comprehend the nature of forest variation from place to place. This was in accord with the preoccupation of ecologists in temperate countries at that time with the nature of climax communities and with succession. This phase of study culminated with the publication of a masterly synthesis by P.W. Richards of the whole field up to about 1940.[18] Independently, colonial foresters began to delimit blocks of forest to be preserved from felling for agriculture, to control the utilization of forests for timber production, and to develop silviculture. This last involved the application of the centuries old European knowledge about what is today sometimes called 'gap-phase dynamics', namely the ability of different species to regenerate after different degrees of canopy disturbance.

In recent decades the two separate streams have merged to lead to the new synthesis which is a major part of the present book.

Apart from the growing knowledge of tropical rain forests in the Western scientific tradition it must not be forgotten that within the tropics man has lived close to Nature and in intimate contact with tropical forests for millenia. The forests yielded all the products needed for his life, and he learned how to grow crops on inherently infertile rain forest soils, by shifting agriculture, moving the fields every 2 or 3 years and allowing forest regrowth to restore site fertility. This discovery was made independently in all parts of the tropical zone. His numbers were never large.

The era of European exploration of the world followed by the Industrial Revolution led to increasing human impact, which has increased continually till the present day (Figs. 1.7, 1.9). The evolution of medical knowledge in the West, plus the development of powerful drugs, has this century removed most of the health hazards of the humid tropics so that death rates have diminished and life expectancy increased, both dramatically. This has added the new pressure on tropical forests of much higher and rapidly increasing

**Fig. 1.4**. Lowland evergreen dipterocarp rain forest in profile (Brunei), with *Dipterocarpus crinitus* right centre and *Shorea curtisii* to its left. Without the scale object the reader would not realize the huge size of these trees.

**Fig. 1.5.** Profile diagram of lowland evergreen dipterocarp rain forest, Brunei. Ridge crest plot 60 × 7.5 m, all trees over 4.5 m tall shown. Mature phase forest except for extreme right hand end. (From Ashton 1965, in Whitmore 1984a, Fig. 1.6; see latter for species' identification.)

human populations (Fig. 10.1). The technological development of reliable machines for road building and log hauling, of chain saws for tree felling, and of bulldozers for land-clearance since World War 2 have made it possible to remove tropical rain forests on a scale and at a rate that was previously impossible. The forest frontiers have been rolled back. What seemed limitless forests a few decades ago are now seen as finite and vulnerable. Even only a third of a century ago, when my own Odyssey began, tropical rain forests seemed boundless. I descended the Amazonian flank of the Andes in Ecuador on muleback to investigate montane forest zonation, a journey which now takes an hour by bus. Then I travelled widely through the Solomons in the western Pacific by schooner, and collected plants never seen by science on sparsely

inhabited islands where the rain forest came down to the wild coconuts leaning over the sandy beach. Later I explored the eastern part of the Malay peninsula, poling up rivers by prahu to the head of navigation before walking for several days to the peaks cresting the watershed.[19] Now one flies to those lands from London in only a day or so and can next day be in the patches of jungle which remain, arriving by dump truck along a muddy logging road. There is more general and scientific interest in tropical rain forests than ever before and this new ease of access is part of the reason. So let us now turn in Chapter 2 to a close examination of the tropical forest zone and then continue with analysis of its plants, animals, dynamics, and present status.

**Fig. 1.6.** Emergent kapok, *Ceiba pentandra* var. *caribaea*; riverine forest near Iquitos, Peru. Subsequently all felled to supply a short-lived plywood industry.

This species is one of the biggest and commonest emergents of the Amazonian rain forests (Gentry and Vasquez 1988) and occurs also in Africa (Fig. 3.30).



**Fig. 1.7.** Lowland semi-evergreen rain forest penetrated by logging road. Lower Amazon, Jari, Brazil.

**Fig. 1.8.** Giant herbs, here the aroid *Colocasia gigantea* at Langkawi, Malaya, are a distinctive feature of the lowland humid tropics.



**Fig. 1.9.** Lowland evergreen dipterocarp rain forest in profile, beside a newly built telecommunications tower access-track, Malaya. Emergent *Canarium* and *Shorea* but no other distinct strata. Note man.

# 2

# What are tropical rain forests?

## 2.1. Tropical moist forests and their climates

The German botanist A. F. W. Schimper was one of the great nineteenth century naturalists. In 1898 he wrote a monumental book, translated in 1903 into English as *Plant geography upon an ecological basis*, which built upon the hundred years and more of European scientific discoveries in the tropics. To Schimper we owe the term tropical rain forest (*tropische Regenwald*) for the forests of the permanently wet tropics. He recognized in total four major sorts of woody vegetation in the tropics. Rain forests, then in progressively drier and more seasonal climate, monsoon forests, savanna forests, and thorn forests. In still drier climates non-woody vegetation, tropical grasslands, and deserts, were recognized. This classification is still useful as an outline framework in all parts of the tropics. For most purposes Schimper's great groups provide too coarse a classification of vegetation and it is useful to have more finely defined classes. These are called formations, and in all six of Schimper's groups several can be recognized. A vegetation formation is defined on its structure and on the physiognomy of its component plants. For tropical forests the structural properties include the height of the trees, whether they tend to have their crowns in layers, and the presence of different kinds of climbers and epiphytes. The physiognomic properties include whether the trees are buttressed, their crown shape, the nature of the leaves, (size, shape, thickness, margin), whether the forest is evergreen or, if not, how strongly deciduous, and where on the trees flowers and fruits are borne. Using these criteria different forest formations can be defined and are found to occur in many different places.

Amongst the various tropical rain forest formations are the most structurally complex and diverse land ecosystems that have ever existed on earth, with the greatest numbers of co-existing plant and animal species. In species richness they are only rivalled by coral reefs. These lofty forests are the apex of creation.

### Climate

Constant high temperature is characteristic of tropical climates, and climates in which the mean temperature of the coldest month is 18 °C or over, is often used as a definition. This excludes some tropical montane areas and a difference of less than 5 °C between the mean temperatures of the warmest and coldest months is sometimes used as an alternative definition. Rainfall is the second most important factor, and its amount, and even more important its distribution through the year, define different tropical climates. Night is the winter of the tropics, because the diurnal range of mean daily temperature exceeds the annual range and is greater in the drier months.

Rain forests develop where every month is wet (with 100 mm rainfall or more), or there are only short dry periods which occur mainly as unpredictable spells lasting only a few days or weeks. Where there are several dry months (60 mm rainfall or less) of regular occurrence, monsoon forests exist. Outside Asia these are usually called tropical seasonal forests. They are slightly less lofty but with more even canopy top, and the bigger trees are mostly deciduous, although perhaps only briefly. They have fewer dependent climbers and epiphytes, and are less species rich.

The blanket term tropical moist forest was coined in 1976[20] to cover both rain and monsoon/seasonal forests, Schimper's first two great

groups, which together comprise the tall, closed-canopy forests of the wet tropics. Tropical moist forest has proved a useful grouping for analyses of the rate of forest disappearance (which will be discussed in Chapter 10), because the exact boundary between rain and seasonal forests is hard to pinpoint and because individual nations seldom distinguish them. To the biologist, however, there are major differences, and this book is about tropical rain forests, those which occur in the ever wet (perhumid) climates, with only passing mention of monsoon forests.

The climates in various parts of the rain forest belt are shown in Fig. 2.1 using the useful pictorial device of Climate Diagrams devised by Walter and Lieth.[21] Note the distinction, even within the rain forest belt, between places with no dry season (e.g. much of the Indo-Malayan forests and the western Amazon), and those where there is a slight dry season (e.g. West Africa and the eastern Amazon). One savanna forest site is also shown (Tamale in Ghana) to demonstrate the much lower and less evenly distributed rainfall of the seasonal tropics.

The Climate Diagrams depict average climate. For plants and animals extremes are often more important than means, even when only of rare occurrence. For rain forests unusually prolonged dry periods are of particular significance, for example as triggers for flowering (section 3.3), or because drought can actually kill plants or make the forest flammable (section 7.6).

Forests, because of their stature, have internal microclimates that differ from the general climate outside the canopy. These are discussed more fully in section 7.1. In general terms, it is cool, humid, and dark near the floor of a mature patch of forest, progressively altering upwards to the canopy top. Different plant and animal species have specialized to the various forest interior microclimates, as will be seen below.

## Occurrence of tropical rain forests

Tropical rain forests occur in all three tropical land areas (Fig. 2.1). Most extensive are the American or neotropical rain forests,[22] about half the global total, $4 \times 10^6 km^2$ in area, and one-sixth of the total broad-leaf forest of the world.[23]

These occur in three parts, of which the largest lies in the Amazon and Orinoco basins. Second is a block which lies across the Andes on the Pacific coasts of Ecuador and Colombia, extending northwards through middle America as far as Veracruz in southernmost Mexico (19°N). The Atlantic coast of Brazil has a third block, a strip less than 50 km wide on the coastal mountains, extending beyond the tropics to the vicinity of Rio de Janeiro (c. 23°S). It has now been over 99 per cent destroyed (Fig. 10.12). It merges southwards into subtropical rain forest of simpler structure and different flora, but in a way we shall never now be able to define. Brazil is the nation with more rain forest than any other.

The second largest block of tropical rain forest occurs in the Eastern tropics, and is estimated to cover $2.5 \times 10^6 km^2$. It is centred on the Malay archipelago, the region known to botanists as Malesia.[24] Indonesia[25] occupies most of the archipelago and is second to Brazil in the amount of rain forest it possesses. The Eastern rain forests extend beyond Malesia into the Pacific and southwards as a narrow broken coastal strip in Queensland, northeast Australia, in a similar position to the Atlantic coast forests of Brazil. As in Brazil, this forest extends beyond the tropics, southwards into New South Wales. Close study of the merging zone has shown that towards their temperate limit tropical rain forest formations become increasingly restricted to the wettest sites and the deepest, most friable, and most fertile soils.[26] The Malesian forests extend northwards up the Malay peninsula into continental southeast Asia, Burma, Thailand, and Indo-China. Again at the boundary they probably occur as a mosaic and occupy the 'best' sites, though we lack detailed studies. There is also an ill-defined change to subtropical rain forest. Between 92° and 97°E, on the great south wall of the Himalaya in upper Burma, Assam, and southern China, rain forest reaches further away from the Equator than anywhere else, attaining 26°N.[27] There are further outliers, in southwest Sri Lanka centred on Sinharaja, and also on the Western Ghats of India where seasonality is strong.

Africa has the smallest block of tropical rain forest, $1.8 \times 10^6 km^2$. This is centred on the Zaire basin, reaching from the high mountains at its
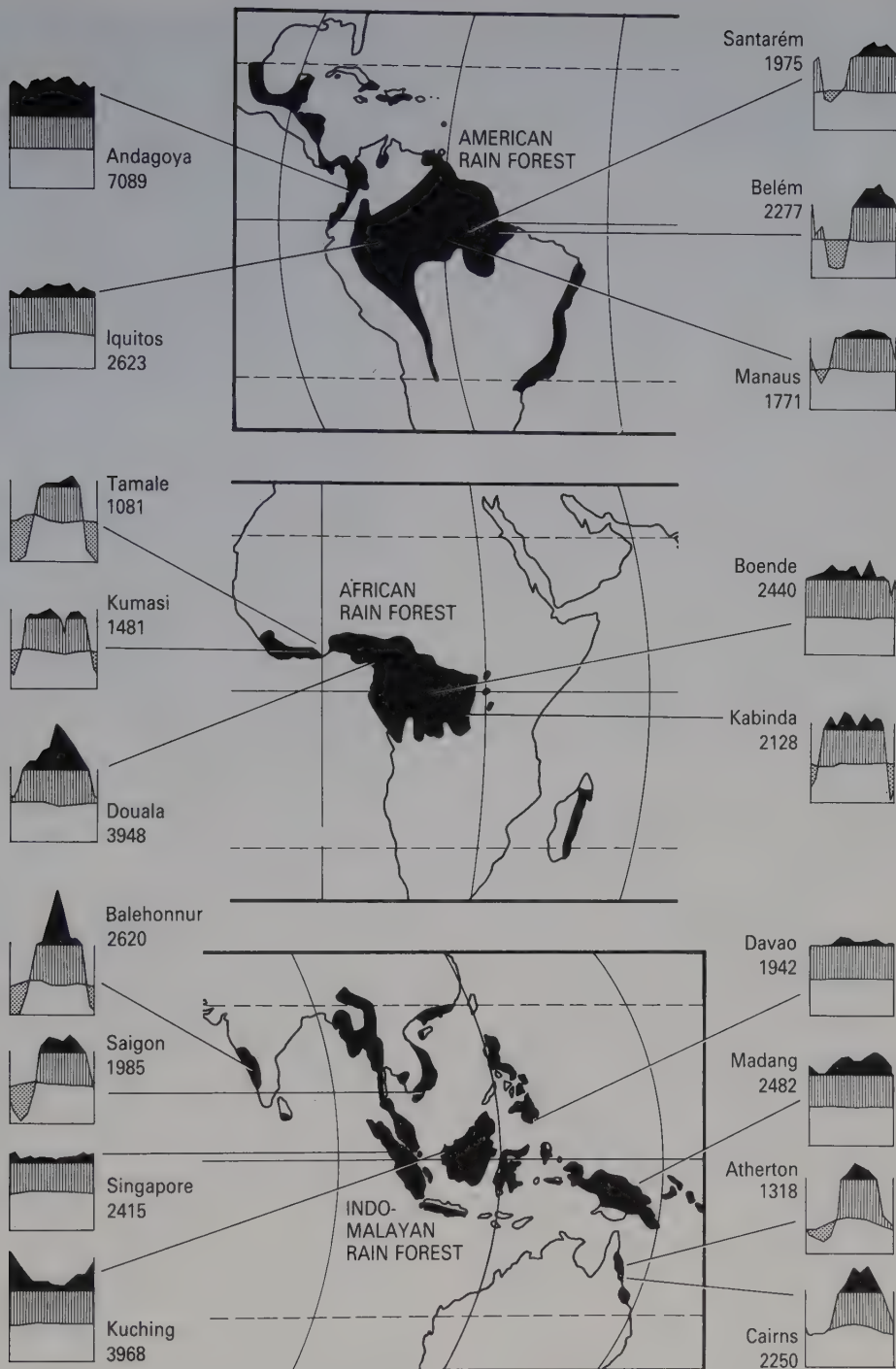
**Fig. 2.1.** Tropical rain forest, distribution and climate. (After White 1983; Whitmore 1984*a*; Walter and Lieth 1967.)

The Climate Diagrams show dry periods as dotted and rainy periods as hatched (or where monthly rainfall exceeds 100 mm shown black at 1/10 scale). Long-term mean annual rainfall (mm) is shown in figures. Dry periods which occur irregularly scattered through the year do not show up on these diagrams because they are based on long-term means.

eastern limit westwards to the Atlantic Ocean, with outliers in East Africa. It extends as a coastal strip into West Africa, but woodlands reach the coast at the so-called Dahomey Gap.[28] There are tiny patches of rain forest on the east coast of Madagascar and in the Mascarenes. Outside the Zaire core the African rain forests have been extensively destroyed.

## 2.2. The forest formations

From a manned satellite or high flying aeroplane the earth is seen to have a sombre, dark, blue-green girdle about the Equator, just glimpsed through breaks in the cloud. There is considerable variation from place to place in this rain forest mantle due to the distinct forest formations. A forest formation, as described above, is recognized by a particular combination of vegetation structure and physiognomy regardless of flora. Convergent evolution has occurred because different species in the three land areas have evolved similar responses to particular environments. In many cases we still do not understand what facet of the environment evokes a particular response, but sometimes we do, as is discussed further in relation to features of montane and heath forests in sections 8.4, 8.5.

The forest formations occupy different physical habitats and these are mostly sharply bounded, but where this is not so there is a merging zone.

The formations can be grouped for convenience according to the main physical characteristics of their habitats (Table 2.1). This is an arbitrary arrangement but gives a useful hierarchy. The naming of vegetation types is always problematical. In the case of tropical rain forest formations the names (listed in Table 2.1) reflect site and the structure and physiognomy of the formation.

The first division is between climates with a dry season and those that are perhumid. The second division is a crude measure of soil water availability, and distinguishes swamp from dryland forests. The third division is on soils and, within dryland forests, distinguishes those on parent materials with atypical properties—peat, quartz sand, limestone, and ultrabasic rocks—from the widespread 'zonal' soils, mainly ultisols and oxisols. Finally there is a division of the forests on zonal soils by altitude.

In this scheme a few formations are defined by physical habitat as well as vegetation structure and physiognomy, for example forest over limestone. The overall result is a set of easily recognized forest formations with memorable names that say something about the most distinctive characteristics of the formation. It is a pragmatic scheme of rain forest classification and the formations can be recognized throughout the humid tropics although many different regional names have been applied. For example in Brazil freshwater swamp forests are called varzea or igapo.

This book is only a primer or introduction to rain forests and descriptions are given just to the more extensive forest formations.

### Tropical lowland evergreen rain forest

*Description.* (Figs. 1.4–1.7, 2.2–2.4) This is the most luxuriant of all plant communities. It is lofty, dense, evergreen forest 45 m or more tall, characterized by the large number of tree species which occur together. Gregarious dominants (consociations) are uncommon and usually two-thirds or more of the upper-canopy trees are of species individually not contributing more than 1 per cent of the total number. This formation is conventionally regarded as having three tree layers (see pp. 25–6): the top layer of individual or grouped giant emergent trees, over a main stratum at about 24–36 m, and with smaller, shade-dwelling trees below that. Ground vegetation is often sparse and mainly of small trees; herbs are patchy. Some of the biggest trees have clear boles of 30 m and reach 4.5 m girth, and may be deciduous (Fig. 3.19) or semi-deciduous without affecting the evergreen nature of the canopy as a whole. Boles are usually almost cylindrical (Fig. 3.28). Buttresses (Figs. 3.30–3.32) are common. Cauliflory (Fig. 1.2) and ramiflory (Fig. 5.2) are common features. Pinnate leaves (Fig. 2.5) are frequent; leafblades of mesophyll size (Fig. 3.25) predominate. Big woody climbers (Fig. 3.14), mostly free-hanging, are

**Fig. 2.2.** Lowland rain forest with luxuriant aroids; *Monstera deliciosa* (cheeseplant, left) and *Philodendron* sp. (right), showing their cord-like pendent roots. (Kerner and Oliver 1895, Fig. 423.)

Table 2.1
*The formations of tropical moist forests*

| Climate | Soil water | | Soils | Elevation | | Forest formation |
|---|---|---|---|---|---|---|
| Seasonally dry | Strong annual shortage | | | | | Monsoon forests (various formations) |
| | Slight annual shortage | | | | | Rain forests: **Semi-evergreen rain forest** |
| Ever-wet (perhumid) | Dryland | | Zonal (mainly oxisols, ultisols) | Lowlands | | **Lowland evergreen rain forest** |
| | | | | Mountains | (750) 1200–1500 m | **Lower montane rain forest** |
| | | | | | (600) 1500–3000 m (3350) m | **Upper montane rain forest** |
| | | | | | 3000 (3350) m to tree-line | Subalpine forest |
| | | | Podzolized sands | Mostly lowlands | | **Heath forest** |
| | | | Limestone | Mostly lowlands | | Forest over limestone |
| | | | Ultrabasic rocks | Mostly lowlands | | Forest over ultrabasics |
| | Water table high (at least periodically) | Coastal salt-water | | | | Beach vegetation Mangrove forest Brackish water forest |
| | | Inland fresh water | Oligotrophic peats | | | **Peat swamp forest** |
| | | | Eutrophic (muck and mineral) soils | ±Permanently wet | | **Freshwater swamp forest** |
| | | | | Periodically wet | | **Freshwater periodic swamp forest** |

Those shown bold are discussed in the text

**Fig. 2.3.** Lowland evergreen dipterocarp rain forest on hill slopes, Selangor, Malaya, at about 800 m elevation. The giant emergent trees 50 m or more tall are *Shorea curtisii*, clumped on spur ridges, and showing the cauliflower-like crowns typical of many Dipterocarpaceae.
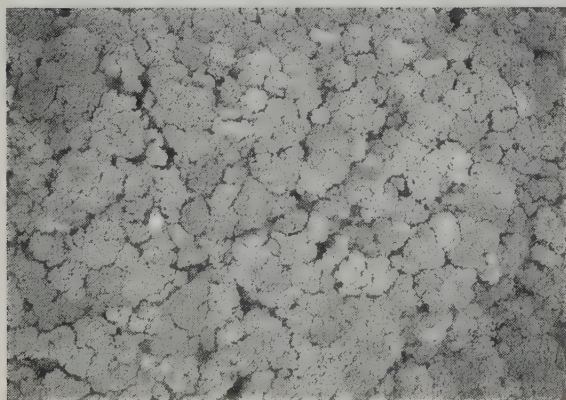


**Fig. 2.4.** Lowland rain forest, Caroni basin, Venezuela. This forest has no emergent trees, the canopy top is fairly flat, and the crowns of the numerous species are nested closely together but mostly with a small surrounding space.



**Fig. 2.5.** Pinnate leaves are a common feature of lowland rain forest; *Canarium sp.* Guandong, China.

frequent to abundant and sometimes also bole climbers (Fig. 3.16). Shade and sun epiphytes (Figs. 3.20, 9.1) are occasional to frequent. Bryophytes are rare.

All other rain forest formations differ from this in having simpler structure, sometimes with fewer life forms, and fewer species.

*Habitat and occurrence.* Tropical lowland evergreen rain forest occurs in perhumid lowland climates where water stress is intermittent or absent, from sea-level to *c.* 1200 m on dryland sites. It is the main lowland formation of the Eastern tropics and also occupies western Amazonia plus the Pacific coast of South America. In Africa it is restricted to three small blocks near the coast of West Africa, between Guinea and Liberia and Cameroon and Gabon.[29] On the Climate Diagrams (Fig. 2.1), all sites with this formation have no regular annual dry season.

## Tropical semi-evergreen rain forest

*Description.* Semi-evergreen rain forest is a closed, high forest in which the biggest emergent trees sometimes attain 45 m in height. It includes both evergreen and, in the top of the canopy, deciduous trees, in an intimate mixture but with a definite tendency to gregarious occurrence. Deciduous trees may comprise up to one-third of the taller trees, though not all are necessarily leafless at the same time. The number of species is high, but less so than in evergreen rain forest. Buttresses continue to be frequent and occur in both evergreen and deciduous species. Bark tends to be thicker, and rougher and cauliflory and ramiflory rarer. The stature tends to be slightly less than evergreen rain forest with emergents as scattered individuals which are sometimes rare. The canopy is sometimes locally stratified. Big woody climbers tend to be very abundant. Bamboos are present. Epiphytes are occasional to frequent and include many ferns and orchids.

*Habitat and occurrence.*[30] Where there is a regular annual period of moisture stress, either due to rainfall seasonality or particular soil conditions, this replaces the previous formation. It occupies the lower Amazon and most of the African rain



**Fig. 2.6.** The rain forest margin, northeast Queensland, Australia.

Lowland semi-evergreen rain forest in the foreground sharply merging into wet sclerophyll forest with emergent *Eucalyptus grandis* in the background. The view is looking westwards, away from the coast, to increasingly dry climates.

forest block, including the whole Zaire basin. It occurs today as a narrow fringe around the main Eastern rain forest block, and also forms the outlier in India and most of the Australian tropical rain forest (Fig. 2.6). It was probably more extensive in parts of continental southeast Asia in the past but has been reduced to its present extent by human activities. This is probably the formation that occurs in middle America. The south China rain forest is, however, in part the evergreen formation.[31] The occurrence of a dry season is clearly shown in the Climate Diagrams of Fig. 2.1 except in the Zaire basin where dry periods are so irregular in occurrence that they do not show up on these long-term mean records.

## The montane rain forests

*Description and habitat.* (Figs. 2.7–2.10) As one climbs a tropical mountain one successively encounters forests of different structure and physiognomy (Table 2.2). The most dramatic change, which usually occurs over a short distance, is from mesophyll-dominated forest with an uneven billowing canopy surface to a lower, more even, often pale-coloured, microphyll-dominated canopy, of more slender trees, usually with gnarled limbs and very dense subcrowns. This is upper montane

rain forest. It is clearly distinctive both from the air and to the traveller on foot. This formation is often only 10 m tall or less, and its shorter facies are sometimes called elfin woodland. The trees may be heavily swathed in bryophytes and filmy ferns and the formation is then known as mossy forest (though liverworts dominate). Peat often forms, sometimes with the bog moss *Sphagnum*. On small mountains upper montane rain forest abuts on lowland rain forest, but on bigger ones an intermediate formation, lower montane rain forest, occurs and this has a broad ecotone against the lowland formation. On the highest peaks upper montane rain forest itself is replaced upwards by a shorter more gnarled formation with even tinier leaves (nanophylls) known as subalpine forest, of which good descriptions exist for New Guinea,[32] but which is much more extensive in the Andes. The tree line on the biggest mountains is at *c.* 4000 m. It is often depressed by fire. Above it beyond the climatic limits of trees occurs alpine vegetation, an edaphically determined mosaic of shrub heath, moss tundra, fern meadow, and grassland, called paramo in the Andes. These treeless landscapes extend up to the snowline at *c.* 4500 m.

On large mountains all the forest formations occur to higher elevation than on small ones and outlying spurs. This is the so-called *Massenerhebung* or mass elevation effect, first described for the Alps. In the tropics the compression and depression of the forest belts on small mountains seems mainly associated with lowering in the level at which cloud habitually forms.

The changes in forests and their environment with elevation are analysed further in section 8.5.

*Occurrence.* The Eastern tropics are very mountainous and many descriptions exist of the extensive montane forests and their zonation.[33] There are fewer descriptions for the Andes, although the complete series of formations occurs on both

Table 2.2

*Characters of structure and physiognomy used to define the principal montane forest formations*

| Formation | Tropical lowland evergreen rain forest† | Tropical lower montane rain forest | Tropical upper montane rain forest |
|---|---|---|---|
| Canopy height | 25–45 m | 15–33 m | 1.5–18 m |
| Emergent trees | Characteristic, to 60(80) m tall | Often absent, to 37 m tall | Usually absent, to 26 m tall |
| Pinnate leaves | Frequent | Rare | Very rare |
| Principal leaf size class of woody plants‡ | Mesophyll | Mesophyll | Microphyll |
| Buttresses | Usually frequent and large | Uncommon, small | Usually absent |
| Cauliflory | Frequent | Rare | Absent |
| Big woody climbers | Abundant | Usually none | None |
| Bole climbers | Often abundant | Frequent to abundant | Very few |
| Vascular epiphytes | Frequent | Abundant | Frequent |
| Non-vascular epiphytes | Occasional | Occasional to abundant | Often abundant |

From Whitmore (1984a, Table 18.1)
† Included for comparison
‡ Following Raunkiaer (1934)

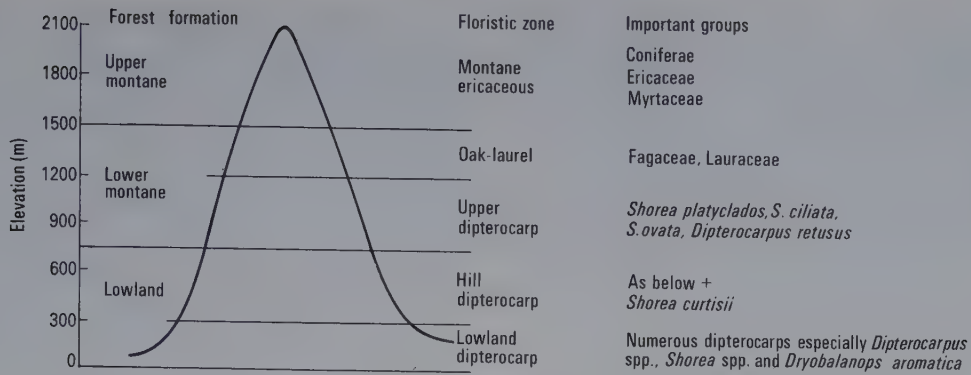| Elevation (m) | Forest formation | Floristic zone | Important groups |
|---|---|---|---|
| 2100 | Upper montane | Montane ericaceous | Coniferae Ericaceae Myrtaceae |
| 1800 | | | |
| 1500 | | Oak-laurel | Fagaceae, Lauraceae |
| 1200 | Lower montane | | |
| 900 | | Upper dipterocarp | *Shorea platyclados, S. ciliata, S. ovata, Dipterocarpus retusus* |
| 600 | Lowland | Hill dipterocarp | As below + *Shorea curtisii* |
| 300 | | | |
| 0 | | Lowland dipterocarp | Numerous dipterocarps especially *Dipterocarpus* spp., *Shorea* spp. and *Dryobalanops aromatica* |

**Fig. 2.7.** Forest zones on the main mountains of Malaya. (Whitmore 1984*a*, Fig. 18.1.)



**Fig. 2.8.** Upper montane rain forest, Mount Benom, Malaya.

Note flattish canopy top, and trees with dense subcrowns of crowded foliage and small leaves. The big trees are *Leptospermum flavescens*; their gnarled limbs are another distinctive feature of this forest formation.

**Fig. 2.9.** *Leptospermum flavescens* with an undergrowth of low bushes, ferns, and sedges. A dry, open facies of upper montane rain forest; Mount Benom, Malaya. Man for scale.



**Fig. 2.10.** Upper montane rain forest, Mount Nokilalaki, Sulawesi, 2275 m elevation.

The trees are swathed in filmy ferns and bryophytes. This facies is often loosely called 'mossy forest', though the bryophytes are mostly liverworts.

flanks and over large areas. The fullest studies have been made on Jamaica in the Caribbean where zonation is compressed. Montane rain forests are least extensive in Africa, where they occur in Cameroon and at the eastern fringe of the Zaire river basin. Africa has the most extensive seasonally dry tropical montane woody vegetation (forests, bushlands, thickets, and shrublands), whose description is beyond the scope of this book.[34]

## Heath forest

*Description.* (Figs. 2.11–2.13).

Even the botanically inexperienced casual wanderer will notice the change when he enters the kerangas forest . . . the storey formed by large saplings and small poles predominates and forms a tidy and orderly but forbidding phalanx which is dense and often difficult to penetrate. The canopy is low, uniform and usually densely closed with no trace of layering . . . brownish and reddish colours prevail in the foliage of the upper part of the canopy and (the forest) . . . appears considerably brighter.

Thus wrote E. F. Brunig, foremost student of the Asian heath forests, about the Bako National Park, Sarawak.[35] He also recorded the predominance of microphylls over mesophylls, and that many leaves are sclerophyllous, often held obliquely or vertically, often in dense clusters, and either waxy grey or highly reflective. Big woody climbers are rare but not slender wiry ones. Epiphytes are common. Myrmecophytes (Fig. 5.11) and insectivorous plants may be abundant, including in Asia the pitcher plants *Nepenthes* (Fig. 4.7).

**Fig. 2.11.** Heath forest with very even canopy top and small crowns, interdigitated with evergreen lowland dipterocarp rain forest in interior Sarawak.



**Fig. 2.13.** *Calophyllum incrassatum* in the Bako heath forest, showing its characteristic shiny, vertically-held leaves. Many species in heath forest have thick, leathery leaves (sclerophylls) like these.

Figs. 2.12, 2.13 both show species with adaptations to minimize foliage water loss and heat load (see section 8.4).



**Fig. 2.12.** Open stunted heath forest at Bako, Sarawak. The tree with feathery foliage massed as dense subcrowns is *Casuarina nobilis*. See Fig. 2.13.

*Habitat and occurrence.* Heath forest occurs on soils developed from siliceous sand, either coastal alluvium or weathered sandstones. These become podzolized. They are low in sesquioxides and so are poorly buffered, and are highly acidic (pH less than 4.0). They are frequently of coarse texture and freely draining. The streams draining heath forest are black, or tea-coloured when viewed by transmitted light (due to the presence of organic colloids), and are usually acid with a low cation content.

The most extensive heath forests are in the upper reaches of the Rio Negro (appropriately named) and Rio Orinoco in South America. In Brazil they are known as campina, campinarana, caatinga Amazônica, or campina rupestre. There has been intensive study of them at the famous San Carlos research centre in southern Venezuela, but they only represent 6 per cent of the Brazilian Amazon rain forests. The description of the Guyana heath

**Fig. 2.14.** Mangrove forests are a forest formation that occurs on accreting coasts in all parts of the tropics. They have several peculiar features of structure and physiognomy, for example stilt roots (seen here on *Rhizophora apiculata* in Malaya), and viviparous reproduction. They are floristically much poorer than most other forest formations, with one family Rhizophoraceae predominant amongst the trees. Mangrove plants have specialized physiological mechanisms to enable them to live in salt water. Mangroves are disappearing fast as land is reclaimed for building (e.g. Singapore), or for prawn ponds or salt pans. They are the breeding ground for the marine life on which coastal fisheries depend and it is being increasingly realized that their destruction has serious repercussions. Fuller accounts can be found in Clough (1982) on salt balance, Lugo and Snedaker (1974) on ecology, and Tomlinson (1986) on taxonomy.

forest dominated by wallaba, *Eperua falcata*, by T. A. W. Davis and P. W. Richards,[36] is one of the classic works of rain forest ecology. There are extensive heath forests in Kalimantan, Sarawak, and Brunei in Borneo, where they are called kerangas. The other principal occurrences are small areas in Malaya, and on coastal sands in Africa in Gabon, Cameroon, and Ivory Coast.

Heath forest is perhaps the most strikingly distinctive lowland rain forest formation. There has been much debate on the extent to which its special features are correlated with either nutrient status or with water relations. These topics are discussed further in section 8.4.

**Fig. 2.15.** Steep limestone hills, here in Malaya in the form of tower karst, are extensive in the Eastern tropics and Caribbean. Limestone carries a distinctive forest formation with several very different facies; for example sheltered enclosed valleys are rich in herbs (especially Gesneriaceae) and epiphytes; and exposed summits, which are prone to desiccation, have a stunted xeromorphic forest with resemblances to the heath forest formation. For fuller details see Whitmore (1984*a*).

## Peat swamp forest

*Description.* This is a forest formation defined more on its special habitat than on structure and physiognomy. The Eastern peat swamp forests have a limited and distinctive flora.

*Habitat and occurrence.* In parts of Sumatra, Malaya, Borneo, and west New Guinea a physiographic setting exists which has favoured the formation of peat. Since sea-level rose at the end of the last Glacial maximum (section 6.2), the rivers have deposited silt as levées and on flood plains. Swamps developed behind the levées and became less saline as their soil level was raised by continuing silt deposition at times of high river level. Mangrove became replaced by inland species whose litter failed to decay in the still salty, high sulphide, waterlogged conditions. This litter turned into peat which has continued to form up until the present day. The result is that now there are domed peat swamps up to 20 km across which are oldest in the centre. These carry up to six different forest types; developed concentrically on the dome (Fig. 2.16), each occurs at a particular height above the water table. The innermost type is an open,

stunted forest. The outer forests reach 50 m tall and are a valuable timber resource.[37] Because deep peat is impossible to use for agriculture, peat swamp forests are likely to remain part of the forest estate. The peat is semi-liquid and low in nutrients because the only input is from rainfall. Peat reaches 13 m thick in the most developed domes. Lowland peat swamp forests also occur in the Americas (including the pegass swamps of Guyana), but have not received detailed study. They are of very limited extent in Africa.

## Freshwater swamp forests

*Description.* (Figs. 2.17, 2.18). Like peat swamp forests these are defined mainly on habitat. They are a very diverse assemblage of forest types flooded by river water, hence with soils richer in plant nutrients than peat swamp forest, and of fairly high pH (6.0 or more). Where flooding is periodic, either daily, monthly, or seasonally, further dimensions of variability are introduced, a group called periodic swamp forests. There may be a few centimetres of peat, or an organo-mineral (muck) soil may occur.
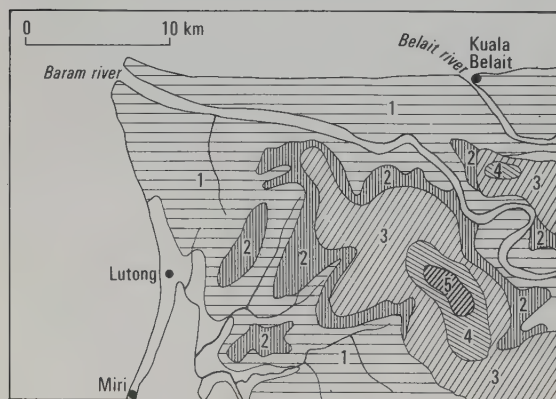


**Fig. 2.16.** The highly developed peat swamp forests of Sarawak are domed and bear a concentric series of different forest types (1–5) from edge to centre. (Whitmore 1984*a*, Fig. 13.5.).

A core taken through the peat at the dome centre contains pollen of the successive communities, with mangrove at the base. This demonstrates that as the dome gets higher by peat accumulation each community is replaced by the next in sequence.



**Fig. 2.17.** Seasonal freshwater swamp forest. Papua New Guinea.

**Fig. 2.18.** Freshwater swamp forest. Papua New Guinea.

*Habitat and occurrence.* The Amazon, which has annual floods and is also influenced by tides to some 600 km inland, has very extensive and diverse freshwater permanent and periodic swamp forests, known as igapo and varzea respectively for white water (silt-laden) and black water rivers. Where unstable banks of alluvium occur which are moved by every annual flood extensive ephemeral grasslands develop during the low water season. It is surprising to the visitor to see this mighty river and its main tributaries flanked by meadows not by forest. The species occurring in swamp forests along black water rivers differ from those along more eutrophic white or clear waters. The alluvial plains of Asia once carried extensive swamp forests but little now remains as these have mostly been cleared for wetland rice cultivation. The Zaire basin is about one-third occupied by swamp forests, many disturbed by man, and little studied.

## 2.3. Forest maintenance—the growth cycle

The discussion so far has been about mature forests. The different formations all have distinctive structure related to which are particular physiognomic features and dispositions of epiphytes and climbers. But the canopy is not all like this, because trees are mortal and eventually die. In reality, the canopy is in a continuous state of flux, with gaps (Fig. 2.19) developing from one of many causes, varying in size from tiny to huge. Gaps are colonized by seedlings which grow up to become saplings and then poles before attaining maturity. In order to analyse this dynamic nature of the forest canopy it is convenient to recognize a forest growth cycle consisting of gap, building, and mature phases, which are arbitrary subdivisions of the continual process of growth.[38] It follows that a forest consists of a mosaic of patches at different phases of the growth cycle (Fig. 2.20). This pattern in space reflects the processes of forest maintenance which continue through time. Where a tree dies of old age, its crown slowly dies back and then the limbs and finally the bole disintegrate. In this case a fourth, degenerate phase to the growth cycle exists. Commonly, however, a tree dies suddenly, struck by lightning or blown

over (Fig. 2.21), or snapped off by wind. Wind may blow over several trees. In an extreme case, windthrow has created long narrow corridors to over 8 km long in Sarawak peat swamp forest. On steep slopes landslides occur, perhaps as a result of an earthquake. Volcanoes create mud flows (lahars) or ash or lava flows. Between 10–20° north and south of the Equator cyclones occur and these periodically clear huge swathes of forest, in the Caribbean, Bay of Bengal region, northeast Philippines, Queensland, and Melanesia. These various causes create canopy gaps of greatly different size and some places are more prone to extensive destruction than others. The forest structural mosaic varies from very fine to extremely coarse.

The Dutch forester F. Kramer created in the lower montane rain forest of west Java artificial gaps of 0.1, 0.2, and 0.3 ha, equivalent to circles of 36, 51, and 62 m in diameter.[39] In the smallest gaps seedlings grew up which had established below the canopy, but in the larger two sizes they were replaced by a new set of different species which were not present before. This is what always happens as gap size increases, and the two

kinds of species are called climax and pioneer, respectively.[40] Climax species can germinate and their seedlings establish below a forest canopy, so climax species can persist in the same place, the seedlings growing up after a gap develops. But if the gap is too big the climax species are replaced by pioneer species which germinate and grow fast after gap formation. Pioneer species cannot germinate, nor can their seedlings survive, below canopy shade. They cannot therefore perpetuate themselves in the same place. Below pioneer trees climax species establish and as the pioneers die off, one by one or in small groups, canopy gaps develop and the next growth cycle is based on these climax species. There is a floristic shift from one suite of species to the other, and this is what is termed succession (Figs. 2.22, 2.23).[41]

Any forested landscape is likely to have a patch somewhere which is recovering from a landslide or from multiple windthrow as a forest of pioneers, so this patch is in a state of succession. Elsewhere climax species will occur. These, as a class, are self-perpetuating, so their regrowth in gaps is cyclic replacement rather than succession. The landscape is in a state of dynamic equilibrium, not changing as a whole although small parts are in continual flux. It has aptly been termed a shifting mosaic steady state.[42]

Forests differ in the gap-forming processes to which they are prone. For example, Papua New Guinea[43] is a land of cyclones, earthquakes, volcanic eruptions, and periodic fires, all of which



**Fig. 2.20.** Canopy phases on 2 ha of tropical lowland evergreen dipterocarp rain forest at Sungei Menyala, Malaya, 1971.

Long narrow gaps result from windfall of single moribund giant trees. Big gaps result from multiple windfall increasing an originally small gap. The extensive area at the north end of building phase forest results from regrowth after partial clearance in 1917. A plan like this is a valuable aid to interpreting forest structure and dynamics.



**Fig. 2.19.** Forest canopy gap formed by the fall of a single large tree. (Hallé *et al.* 1978, Fig. 107.)

The medieval French word chablis is sometimes used to describe the canopy hole, plus the associated damage, and the fallen mass of branches, leaves, and twigs.
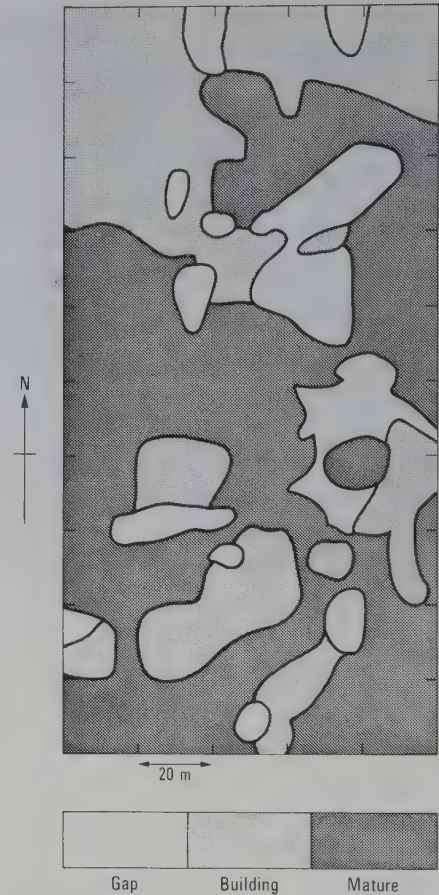
cause catastrophic destruction of big swathes of forest. The mosaic of structural phases is coarse and forests of pioneers are widespread. It is estimated that 8–16 per cent per century of the land surface of Papua New Guinea is disturbed by landslides, and 2 per cent of Panama, another earthquake-prone country.[44] Borneo and the Brazilian Amazon by contrast have very little catastrophic destruction from these natural causes; fine structural mosaics and stands of climax species are widespread.

**Fig. 2.21.** View along a gap created by a single treefall. Note man to right of the upturned roots and soil (the so-called root plate). Sulawesi.

Gap-phase dynamics and the two ecological groups of species, pioneer and climax, will be described more fully in Chapter 7. It seems that most of the world's forests work according to this model.[45] Strongly seasonal tropical forests in which fire is a major factor are probably an exception. It is likely there that after disturbance resprouting rather than regeneration from seed is important; but we have no detailed ecological knowledge on how they work, which is a serious deficiency awaiting an ecologist to apply modern approaches and insights.

## Canopy layers

In this book the term forest canopy is used for the whole plant community above the ground. It is commonly described as being layered or stratified and this is a useful aid to description or analysis although, because the forest is dynamic with patches at all stages of the growth cycle, stratification is a simplification and abstraction.

A mature lowland rain forest has trees of many sizes. The tallest stand head and shoulders above the general level of the canopy and are known as
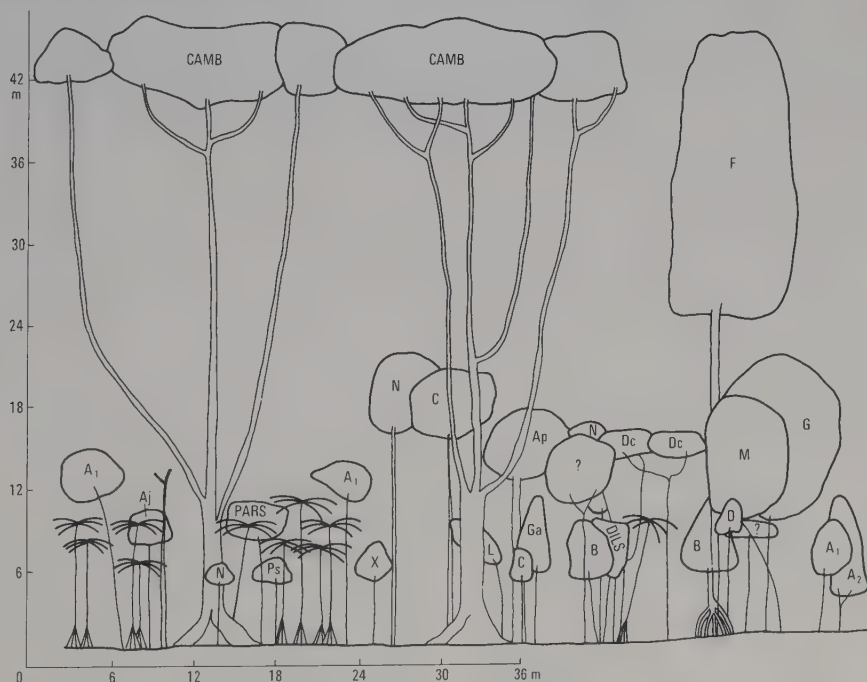


**Fig. 2.22.** Forest on the north coast of Kolombangara, Solomon Islands, dominated by overmature trees of the light-demanding climax species *Campnosperma brevipetiolatum* (CAMB) which is not regenerating itself. (See Whitmore 1974, Fig. 2.3 for full species names.)

This forest resulted from massive disturbance, and unless that is repeated it will change in composition to resemble that of Fig. 2.23, whose species are already present in the lower part of the canopy.

**Fig. 2.23.** Forest on the west coast of Kolombangara, Solomon Islands, dominated by the slow-growing, shade-tolerant climax species *Dillenia salomonensis* (DILS) and *Schizomeria serrata* (SCHS) which are regenerating themselves. (Whitmore 1974, Fig. 2.4 and 1984*a*, Fig. 17.20: see either source for full species list.)

emergents. They occur either alone or as groups. Single kapok trees (*Ceiba pentandra*) which reach immense size in Amazonia, are a common and conspicuous sight viewed from the river (Fig. 1.6). By contrast, the rough, billowing canopy of a west Malesian forest results from groups of emergent species of Dipterocarpaceae (Figs. 2.3, 2.24). Strata have usually been depicted by a profile diagram, a side-view of a strip usually *c.* 60 × 6 m. What such a strip depicts depends on where it lies with respect to the mosaic of structural phases as can be seen from Figs. 2.20 and 2.24. Before their use for tropical rain forests, profile diagrams were used to describe the structure of the forests of south England, which have a very simple structure, just one layer of trees over a shrub and a herb or ground layer (Fig. 2.25). It is probably by

analogy to temperate forests that European scientists sought to see strata in tropical rain forests.

In addition to structural layering, which becomes confused by the growth cycle, different tree species habitually mature at different heights, and whole genera and even some families reach up to different parts of the canopy. For example, most Ebenaceae and Euphorbiaceae are small trees, most Burseraceae, Lecythidaceae and Sapotaceae reach the top of the canopy, and amongst emergents are many Leguminosae and nearly all rain forest Dipterocarpaceae. Far Eastern Myristicaceae are nearly all small trees, but in the neo-tropics there are larger canopy-top species, e.g. the important timber producing genera *Dialyanthera* and *Virola* (Table 10.9). Young individuals, or trees dwarfed because of unfavourable growth con-

**Fig. 2.24.** Profile showing mature (ends) and building phases of the lowland evergreen dipterocarp rain forest at Belalong, Brunei. Plot area 60 × 7.5 m, all trees over 4.5 m tall shown. (Ashton 1964 in Whitmore 1984a, Fig. 2.1; see latter for species names.)

Dipterocarps shown hatched; note how these still have tall, narrow, youthful monopodial crowns in the building phase, which change to sympodial, broader than deep, and with several large limbs in the mature phase.

ditions, obscure such layering and there is no evidence that habitual mature height falls into a small number of discrete classes. Stratification is most prominent in species-poor forest where groves occur of one or a few species, which is why semi-evergreen lowland rain forest is more conspicuously stratified than evergreen (p. 15). Crown form (p. 47) changes from monopodial, deeper than broad, to sympodial, broader than deep, as a big tree matures (Fig. 2.24). Some small tree species remain monopodial to maturity, e.g. Annonaceae, Ebenaceae, and Myristicaceae. It follows that layering of crown shape also occurs, and this is also easily seen on a profile diagram. The forest microclimate alters upwards through the canopy (Fig. 7.1). This probably triggers the metamorphosis of crown form (section 3.2); it also leads to yet another kind of stratification, that of epiphytes and climbers (Fig. 3.17).
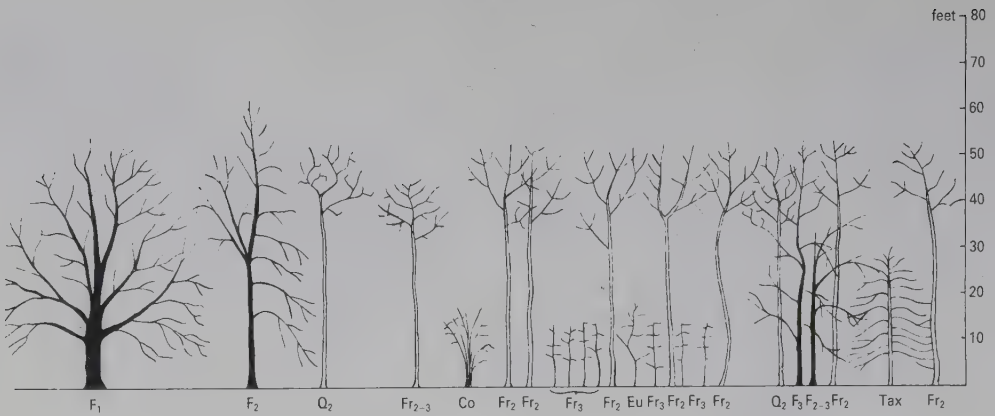
**Fig. 2.25..** Profile diagram of temperate deciduous forest, Sussex, England. F, *Fagus sylvatica* (beech); Co, *Corylus avellana* (hazel); Fr, *Fraxinus excelsior* (ash); Q, *Quercus robur* (oak); Tax, *Taxus baccata* (yew). (After Watt 1924, Fig. 3.)

## 2.4. Floristics

The humid tropics are extremely rich in plant species. Of the total of approximately 250 000 species of flowering plants in the world, about two-thirds (170 000) occur in the tropics. Half of these are in the New World south of the Mexico/ US frontier, 35 000 in tropical Africa (plus 8500 in Madagascar) and 40 000 in Asia, with 25 000 in Malesia. A few plant families are confined to humid tropical climates, e.g. Myristicaceae, the nutmegs; others are strongly concentrated there with a few temperate outliers, e.g. Annonaceae, the soursop family, Musaceae, the bananas, and Ebenaceae, the ebonies (whose temperate species provide the fruits called persimmon).[46]

There are similarities, especially at family level, between all three blocks of tropical rain forest, but there are fewer genera in common and not many species.[47] All three regions have abundant Leguminosae of subfamily Caesalpinoideae. Other big families include Annonaceae, Euphorbiaceae, Lauraceae, Moraceae, Myristicaceae, Rubiaceae, and Sapotaceae. On small areas Annonaceae, Euphorbiaceae, and Rubiaceae are nearly always among the ten most species-rich families in all three regions. America is characterized by numer-

ous Lecythidaceae, the Brazil nut family, with 11 genera, and about 120 species. The most distinctive and unique feature of western Malesia is the abundance and species richness of Dipterocarpaceae.[48] Borneo for example has 287 species and 9 genera, and in many places most of the big forest trees belong to this single family. Conifers have many species in the East (Figs. 2.26, 10.20) and are found at all altitudes. So far only one conifer has been found in the lowland rain forests of Africa and another in tropical America.

In flora Africa has been called 'the odd man out'[49]; there are fewer families, fewer genera, and fewer species in her rain forests than in either America or Asia. For example, there are 18 genera and 46 species of native palms on Singapore island,[50] as many as on the whole of mainland Africa (15 genera, 50 species); Africa has only 4 species of bamboo, and Mt. Kinabalu (4101 m) in northern Borneo has almost the same number of ferns as the African continent.

There are also differences within each rain forest region. Not all species occupy the whole available area despite the absence of physical barriers; for example *Theobroma*, the cocoa genus, is

confined to northwest Amazonia; and many species found in Sumatra do not reach New Guinea. These patterns are thought to have historical causes which will be discussed in Chapter 6. Other patterns are believed to relate to climate. For example, the rain forest flora of Ghana, herbs and trees, alters clinally from west to east across the country, a distance of *c.* 300 km,[51] in parallel with increasing climatic seasonality.

To obtain a more precise picture of differences in species richness, Fig. 2.27 shows the numbers of tree species of 0.1 m in diameter or larger on small plots. The numbers vary from 23 ha$^{-1}$ in Nigeria to 283 at Yanamomo, in the Peruvian Amazon.

On the richest rain forest plots every second tree on a hectare belongs to a different species. It is difficult to conceive a forest richer than the Yanamomo plot, where only 15 per cent of species had more than two individuals and 63 per cent had only one individual.

Species-area curves have been constructed for several forests, and species numbers continue to rise over several hectares (Fig. 2.28).

On a slightly more extended scale a single 50 ha plot at Pasoh, Malaya, contained *c.* 830 species, 20–30 per cent of the total tree flora of the country down to the size measured (10 mm diameter). An enumeration of 6.6 ha spread across 5 × 2.5 km of forest at Bukit Raya, Sarawak had 711 species over 0.1 m in diameter which is about half the trees of this size found in all of Sarawak.

To set these figures in context the whole of Europe north of the Alps and west of USSR has only 50 indigenous tree species and eastern north America has 171.[52]

One component of the extreme species richness of many rain forests is the local endemics, namely species of very limited range.[53] For example many trees collected in Perak, northwest Malaya in the late nineteenth century have never been found elsewhere and, because the lowlands were soon afterwards largely converted to rubber plantations, are almost certainly extinct. The monospecific genus *Burkilliodendron album*, known from one collection from a limestone hill in Perak, has never been seen again and its habitat has been used for road metal. By contrast although the broadleaf forest cover of England is reduced to *c.*

4 per cent no species of woody plant has been lost from the flora.

Despite the great interest everyone has in the amazing plant species richness of tropical rain forests, there are very few total species counts. On a single 100 m$^2$ plot in wet lowland rain forest in Costa Rica 233 vascular plant species were recorded (Table 2.3). This is by far the richest plant community ever enumerated on Earth. In three forests in western Ecuador sample areas ten times bigger (0.1 ha), and each from ten non-contiguous subplots, had totals of 365, 169, and 173 species in perhumid, dry, and slightly seasonal forest respectively.[54] Even if the trees are excluded, all these four samples are amongst the richest plant communities ever encountered with 153, 251, 125, and 105 non-tree species respectively. The Rio Palenque forest of western Ecuador has a total of 1030 species in 80 ha, one-quarter of them endemic; the whole of the British Isles have 1380 seed plant species, which helps put this figure in perspective.

The most nearly comparable species-rich plant communities outside the tropics are the Mediterranean heathlands of the Cape of South Africa (known as fynbos) and of southwest Australia. Here total species numbers are similar to trees alone in rain forest. Chalk grassland in England is extremely rich on a small scale and may have 32–33 species in a 0.5 m$^2$ quadrat, but the total flora of one site of a few hectares is only 50–55 species.[55]

These various data show that meaningful discussions of species richness must specify scale.[56] For example, we may usefully compare richness within rain forests by counting tree species on plots of *c.* 1 ha. This within-community diversity has been called alpha diversity. At the other extreme we can record species richness of a whole landscape made up of several communities, and this has been called gamma diversity. The fynbos is very rich with 8500 species on 89 000 km$^2$. It is made up of a mosaic of different floristic communities, each of which has rather few species. That is to say fynbos has low alpha and high gamma diversity. Within a single floristic community species replace each other from place to place. This gives a third component to richness, known as beta diversity. For example, within lowland rain forest there are differences in species within a
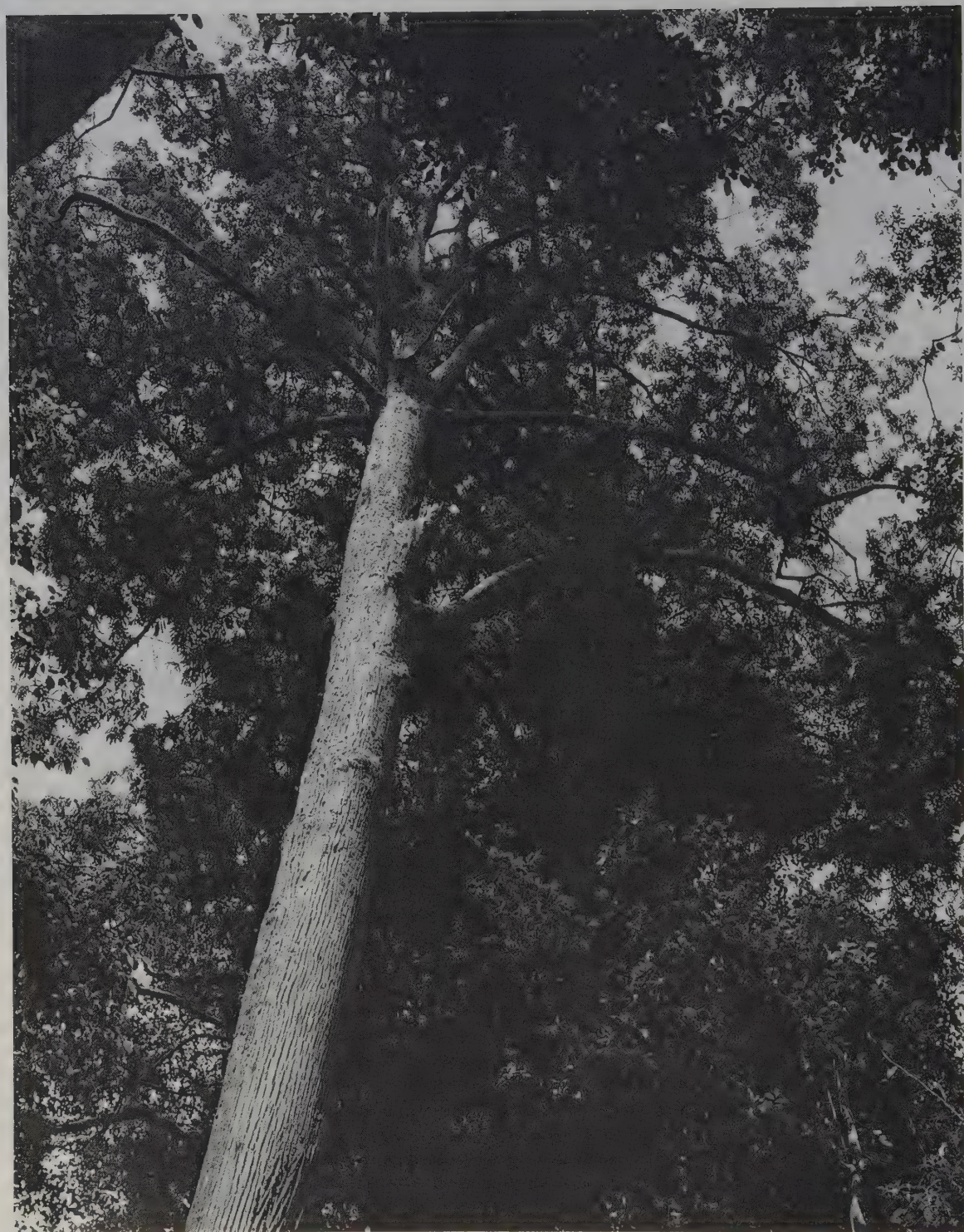
**Fig. 2.26.** The conifer *Podocarpus neriifolius* is a common and valuable timber tree found in lowland and lower montane rain forests throughout Malesia. Note the big, permanent, radial limbs on this mature specimen.
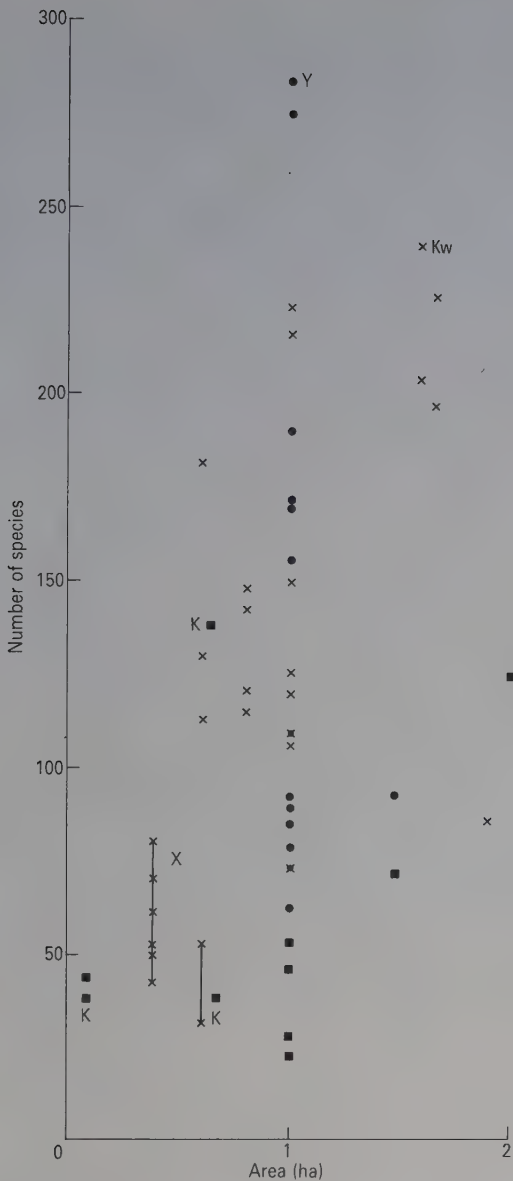
**Fig. 2.28.** Species area curves for tropical lowland evergreen rain forests. (After Whitmore 1984*a* and Genry 1988*b*).

The Yanamomo forest is the richest yet found, every second tree on the hectare plot was a different species. These curves were mostly made by adding together the number of species found on contiguous subplots. See also Figs. 2.29, 6.16*b*.



**Fig. 2.27.** Species richness among trees of 0.1 m in diameter and over on small plots in tropical lowland rain forest. ● America (Y Yanamomo), x Eastern tropics (Kw Kalimantan-Wanariset), ■ Africa (K Korup). Lines connect sample plots that lie close together. (Data of Whitmore 1984*a*, Fig. 1.5; Gentry 1988*b*; Whitmore and Sidiyasa 1986; Whitmore *et al.* 1987.)

Species numbers rise with increasing plot area as is shown on Fig. 2.28. In addition to this basic pattern, the African forests are species-poor except for one at Korup. Most of the Eastern forests are species-rich but the richest forests of all are in America where, however, some are also very species-poor.
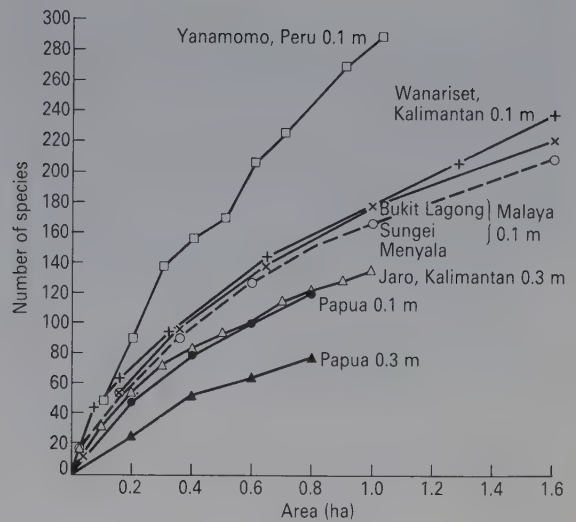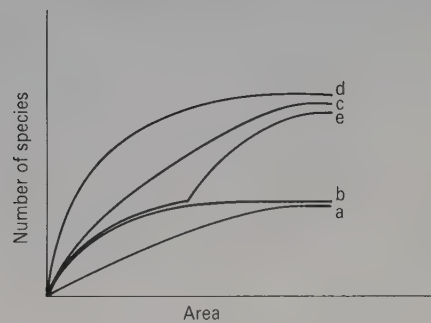


**Fig. 2.29.** The species-area curves of the different kinds of species diversity.

The two species-poor communities (a) and (b) have low alpha diversity and low and high beta diversity, respectively. Communities (c) and (d) by contrast are species-rich and have high alpha diversity (and low and high beta, respectively). Community (e) differs from all the others in having two distinct constituent parts, namely it has higher gamma diversity. The components each resemble (b). See also Fig. 2.28.

single community between ridges, hillsides, and valleys. Figure 7.17 demonstrates how in Amazonian Peru species composition changes as the forest gets older and this is another example of beta diversity. The species richness of chalk grassland is due to high alpha diversity, beta diversity is low.

These different kinds of diversity can be shown on species-area curves (Fig. 2.29). Where numerous species occur on a small area the curve rises steeply. Where the minimum area is large the curve continues to rise a long way before flattening. These represent high alpha and beta diversity, respectively. A change in slope of the curve reflects transition to a different community, so if the curve has a series of steps before it flattens out this shows its full richness contains a component of gamma diversity.

Table 2.3

*Numbers of species and individuals in the different synusiae on a $100\,m^2$ plot in evergreen rain forest near Horquetas, Costa Rica*

|  | Individuals | | Species | |
|---|---|---|---|---|
|  |  | Total |  | Cumulative total |
| Vascular plants: | | | | |
| (a)  Independent (free-standing) plants | | | | |
| Plants ⩽ 1 m tall | 1349 | 132 | | 132 |
| (of which tree seedlings) | | (566) | | (64) |
| Plants 1–3 m tall | 144 | 18 | | 140 |
| (of which trees) | | (134) | | (5) |
| Plants ⩾ 3 m tall | 38 | 18 | | 144 |
| (of which trees) | | (35) | | (4) |
| (b)  Dependent plants | | | | |
| Climbers | | | | |
| bole | 233 | 24 | | 165 |
| woody (free-hanging) | 68 | 20 | | 174 |
| Epiphytes | 339 | 61 | | 233 |
| (of which aroids) | | (90) | | (17) |
| (of which bromeliads) | | (49) | | (8) |
| (of which ferns) | | (87) | | (9) |
| Total all vascular plants | 2171 | | | 233 |
| Bryophyta: | | | | |
| Liverworts | ? | 25 | | |
| Mosses | ? | 7 | | |
| Total all Bryophyta | | | | 32 |

From Whitmore *et al.* (1986, Table 1)
The count was made by a team of 11 people, removing one synusia at a time, and took a total of 192 man-hours. At this rate it would take 10 man-years to extend the plot to a full hectare.

## 2.5. Nature of the tropical rain forest community[57]

Now that the main kinds of variation in tropical rain forests have been described we can consider a question that has been very much discussed by tropical ecologists; namely, whether tropical rain forest is one huge floristic association varying haphazardly from place to place or whether dis-

tinct communities exist.[58] It has been shown in this Chapter that there are in fact numerous kinds of variation. It is possible to arrange them roughly into a hierarchy of diminishing importance.

## Biogeography

Variation can only operate on the species that are present, and over-riding all other reasons for it is the availability of flora. For example, dipterocarps dominate the rain forests of western Malesia and give those forests their unique characteristics which are referred to repeatedly throughout this book.

## Disturbance

The influence of massive disturbance is the second most important factor. Forests regrowing after a cyclone or human destruction, for example, are dominated by pioneer or near-pioneer species (Fig. 2.22)[59] and because trees live a century or more (Fig. 7.30) rare catastrophes can have long-lasting effects.

## Habitat

Major physical habitats bear different forest formations (Table 2.1) and this third cause of variation is of similar importance to major disturbance.

## Variation within the formation

*Topography.* Further down the hierarchy, once these three factors have been allowed for, comes variation within a formation. This tends to be continuous, without sharp boundaries. It results from various causes. One kind is linked to geology, which manifests itself in various ways relating both to topography and to the chemical and physical properties of the soil. Within a rain forest formation it is common for some species to be associated with different topographic situations, especially with valleys or ridge crests. For example, at the edge of swiftly flowing rocky rivers and on their shingle banks, firmly rooted in crevices, is found the synusia of rheophytes (Fig. 2.30). On alluvial valley floors is found another set of species. For example in Sarawak the occasionally flooded levées of well-watered, friable, deep, fertile soil support a very tall forest which includes the group of *Shorea* species producing illipe nuts, plus the Borneo ironwood (*Eusideroxylon zwageri*). An illustration of species that are commonest on ridge crests is the grey-crowned dipterocarp *Shorea curtisii* (Fig. 2.31) and its associate the stemless, prickly, giant bertam palm (*Eugeissona tristis*) in Malaya (Fig. 2.31). However, not all species are strongly linked to topography; Fig. 2.32 gives examples from Panama.

*Soil.* Most rain forest soils are low in plant nutrients and physical factors have a more important role than fertility in determining species ranges. Soil physical factors probably determined which species were more abundant over either granite or shale in a survey of 26 628 trees on 676 ha in Ulu Kelantan, Malaya.[61] At Korup, Cameroon, three large emergent species of Leguminosae/Caesalpinoideae



**Fig. 2.30.** *Homonoia riparia*, a wiry shrub of swiftly flowing rocky rivers, is a typical rheophyte, with linear-lanceolate (willowlike) leaves called stenophyllis. Yunnan, southwest China.

> Rheophytes are a highly distinctive synusia or lifeform community. They are commonest in the tropics, especially in Malesia where they reach greatest abundance in northern Borneo. The life-form is an adaptation to a very difficult habitat, an otherwise empty ecological niche, which has been colonized by only a few unrelated plant families. Van Steenis (1981) gave a full account of these peculiar plants.[60]

**Fig. 2.31.** The dipterocarp *Shorea curtisii* and the big, prickly, stemless bertam palm *Eugeissona tristis* commonly grow together in Malaya.

(*Microberlinia bisulcata, Tetraberlinia bifoliolata, T. moreliana*) form groves *c.* 600 m across which have been shown to be associated with low concentrations in the wet season of extractable soil phosphorus.[62]

*Presence of seedlings.*   Another more subtle level of variation in tree species composition is dependent on the presence of seedlings on the forest floor at the time a gap develops. Different species establish their seedlings better on different microsites (section 7.3). Species also differ in how frequently they produce fruit and hence replenish their seedling bank (section 3.3); for example, the dipterocarp Borneo camphorwood (*Dryobalonops aromatica*), which dominated certain Malayan forests, probably owed its abundance to the 'reproductive pressure' of more frequent fruiting

than other dipterocarps. At this lowest level of variation, which has been named gap-phase replacement, chance plays a strong role: trees must flower, the flowers must set fertile fruit, dispersal must operate, seeds germinate, seedlings establish and survive damage by falling debris or from herbivores, and then a canopy gap must develop over them within a few years before they die in the dimly illuminated forest undergrowth.

As new studies are made to investigate the fundamental problem of the nature of variation from place to place in tropical rain forest, they confirm the model of a hierarchical series of kinds of variation, and illuminate the part of the hierarchy the particular study happens to relate to. Nowadays, attention has increasingly swung away from this problem to address others, which form the subject of the next few chapters.

## 2.6.  What are tropical rain forests?—Chapter summary

1. The wetter tropical climates have closed forests, collectively described as tropical moist forests. Tropical rain forests occur where there is only a short dry season or none. Monsoon (tropical seasonal) forests occur where the dry season is stronger.

2. Distinct forest formations occur in different habitats (Table 2.1), which are usually sharply bounded. They differ mainly in structure and physiognomy and the same formations occur in similar sites throughout the humid tropics.

3. Forests consist of a mosaic of gap-phase, building-phase, and mature-phase forest (Figs. 2.20, 2.24). These phases are arbitrary subdivisions of a continuous forest growth cycle. The pattern of structural phases represents processes of change with time.

4. Climax species regenerate *in situ* and their seedlings grow up in small gaps. Pioneer species

can only germinate and establish in big gaps and cannot establish below a canopy.

5. There are differences in species composition at all scales, between the three tropical areas and within them. Tree species numbers per hectare on small plots vary from *c.* 20 to over 200. Africa is poorest. These factors have historical explanations (Chapter 6).

6. Tropical rain forest communities show variation at a range of scales which can be arranged in a rough hierarchy. Availability of flora comes first, then differences between formations and that resulting from massive disturbance such as cyclones. Within formations variation is more continuous and less obvious and is related to topography (riverine forests and rheophytes are especially distinctive), to soil; as well as to seedling arrival and success at a particular spot, for which there is a strong element of chance.
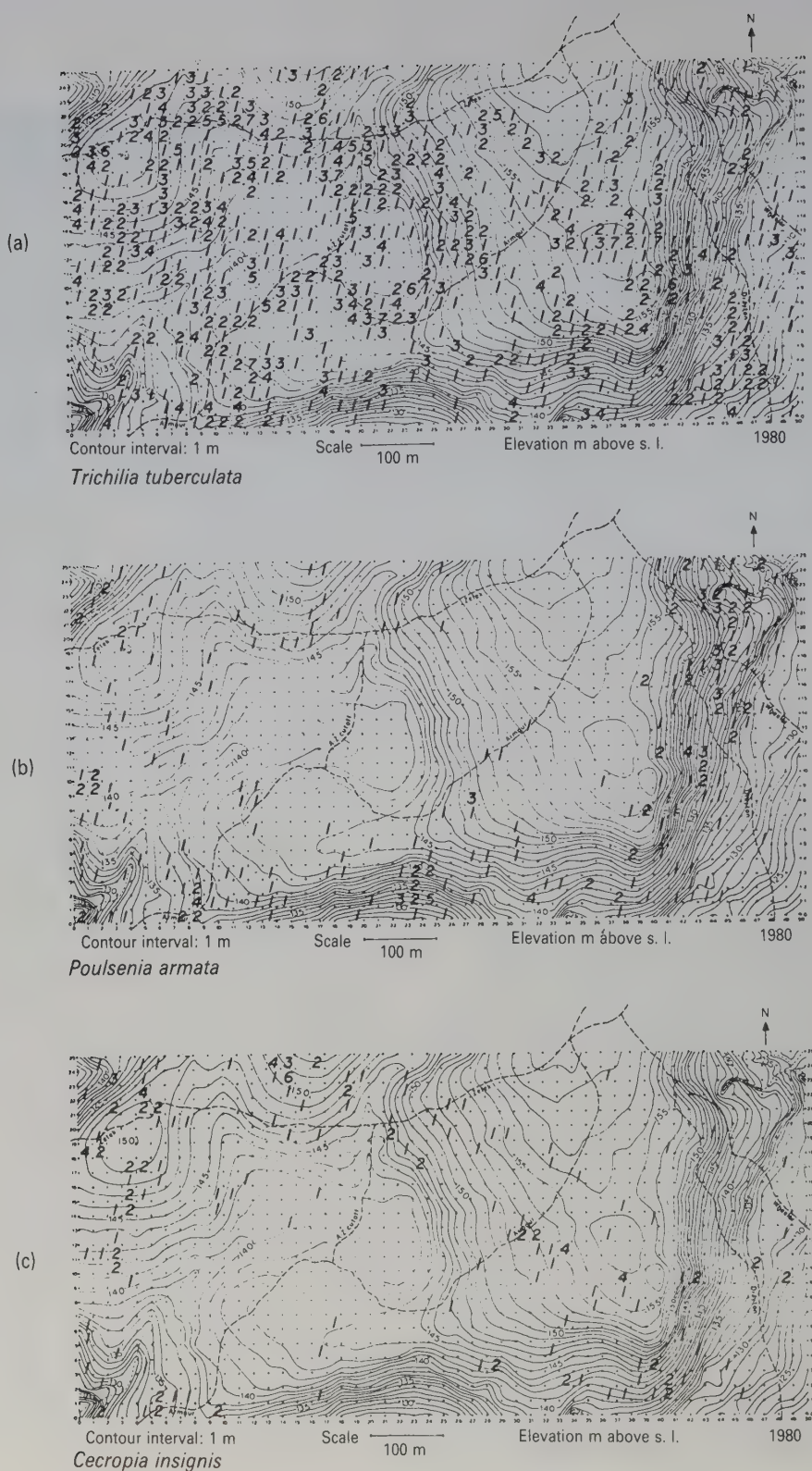
**Fig. 2.32.** Species patterns on a 50 ha plot at Barro Colorado Island, Panama. Trees over 0.2 m in diameter are shown. (a) *Trichilia tuberculata*, the commonest big tree, is ubiquitous. (b) *Poulsenia armata* is largely confined to steep slopes. (c) The pioneer species *Cecropia insignis* occurs in clumps not related to topography but which have developed in canopy gaps. (Hubbell and Foster in Sutton *et al.* 1983.)

The distribution of trees within a rain forest results from many factors which may interact and are not always easy to discover.

# 3

# Plant life

The traveller walks out of an abandoned resthouse on to what was a lawn 18 months before, to find self-sown saplings of *Tectona grandis* [teak] 5 m high. They have long internodes, and leaves the size of dinner plates. He feels like Alice in Wonderland. Or he notices the weeds growing on abandoned farm land, including such objects as *Vernonia conferta*, a composite with vegetative parts like a rosette of *Taraxacum officinale* [dandelion] 3 m across, on a stalk up to 4 m high. . .[63]

The exuberance of plant life in the humid tropics continues to dazzle scientists from the more sober temperate biomes. More 'purple passages' have been penned on lowland evergreen rain forest than any other vegetation type. Trees have a great diversity of form and size and some have the uniquely tropical attributes of huge buttresses or trunk-borne flowers. They support a wealth of climbers and epiphytes: one stands and marvels. Bamboos (Fig. 3.1), palms, cyclanths, pandans[64] (Fig. 3.2), stranglers (Figs. 3.3–3.5, 10.2), and banyans add peculiar extra dimensions. As acquaintance deepens some genera are found to have



**Fig. 3.1.** *Schizostachyum grande* showing the characteristic clumped growth of bamboos. Malaya.

This elegant species becomes abundant in seriously disturbed lowland evergreen rain forest in the mountains at 600–800 m elevation.



**Fig. 3.2.** *Sararanga sinuosa*, showing the typical open branching and strap-like leaves of the Pandanaceae, dendroid monocots of the Old World tropics. Solomon Islands.

**Fig. 3.3.** Strangling fig, showing multiple descending and anastomosing roots wholly obscuring the trunk of the host tree. North Sumatra.

**Fig. 3.4.** Young strangling fig, its host tree still visible. Penang, Malaya.



Trunk of host — Root of parasite

**Fig. 3.5.** The development of a strangling fig (From Corner 1940 as Fig. 2.25 in Whitmore 1984*a*).

Strangling figs occur in all parts of the tropics. In Asia, *Wightia* and *Metrosideros* and in the New World, *Clusia* also have strangling species.

numerous species growing together, distinguished in the forest by details of bole, bark, buttress, and leaf. Dipterocarpaceae in western Malesia are the extreme example. Of *Shorea* M. Jacobs recently wrote[65]:

complete fugues could be composed from the leaves ..., varying in size, thickness, venation and hairs; with countermelodies of fruits and stipules; a single fermenta [flourish] for a particularly large flower; and a tremolo for an aberrant calyx. And from time to time the recurrent melody of the flowers' exquisite scent.

Just so, Fig. 3.6. If the kaleidoscope of striking impressions is analysed we see that trees are the predominant life form, in all sizes from unbranched pygmies with a single apical tuft of leaves (Fig. 3.7) which never get taller than 1–2 m, to emergent giants, which include some of the world's tallest (Table 3.1; Figs. 3.8, 3.9). Shrubs (i.e. woody plants with several main stems) are rare. Forest floor herbs are patchy, and much of the surface is bare except for a, usually thin, layer of leaf litter. On landslips and along rivers giant herbs often form thickets, gingers and Marantaceae everywhere, bananas in Asia (Fig. 3.10), *Heliconia* in America and Melanesia, bamboos in slightly seasonal climates.

Dependent on the free-living autotrophic forest plants are a few heterotrophs. There are many Loranthaceae (mistletoes), as hemiparasitic epiphytes. Santalaceae, which includes the sandalwood (*Santalum*), is a family of small hemiparasitic trees. Full parasites include *Balanophora* (Fig. 3.11) and *Rafflesia* (Fig. 3.12), which in *R. arnoldii*, has the world's largest flower, 1 m in diameter. Saprophytes are uncommon and of only a few families, e.g. Burmanniaceae (Fig. 3.13).



**Fig. 3.6.** Fruits of a miscellany of Dipterocarpaceae. (FAO 1985.)

The family is named from the two-winged fruits of *Dipterocarpus* (Greek di—double, pteron—wing, karpos—fruit). The wings are the flower sepals which become elongated and may be 2, 3, or 5 in number or absent.



**Fig. 3.7.** The monopodial undergrowth treelet *Agrostistachys longifolia*, here seen with an erect tuft of pale green young leaves. Singapore.

Table 3.1
*The World's tallest trees*

| Height (m) | Species (family) | Local epithet | Origin |
|---|---|---|---|
| 111 | *Sequoia sempervirens* (Coniferae) | Californian redwood | California, USA |
| 107 | *Eucalyptus regnans* (Myrtaceae) | blue gum | Victoria, Australia |
| 96 | *Sequoiadendron giganteum* (Coniferae) | wellingtonia | California, USA |
| 89 | **Araucaria hunsteinii** (**Coniferae**) | klinki pine | New Guinea |
| 85 | *Abies nobilis* | noble fir | Washington, USA |
| 84/81 | **Koompassia excelsa** (**Leguminosae**) | menggaris, tualang | Sarawak, Malaya |
| 75 | *Agathis australis* (Coniferae) | kauri | New Zealand |
| 71 | **Eucalyptus deglupta** (**Myrtaceae**) | kamerere | New Britain |
| 70 | **Agathis dammara** (**Coniferae**) | | Sulawesi, Indonesia |

Mainly after Richards (1952)                    † Rain forest species shown bold



**Fig. 3.8.** *Eucalyptus deglupta*, seventh tallest tree species in the world, here *c.* 60 m tall. New Britain.

This is the only rain forest species of *Eucalyptus*. It is a pioneer of riverine alluvium from Sulawesi east to New Britain and is now commonly grown in plantations throughout the humid tropics.

**Fig. 3.10.** Extensive clumps of the wild banana *Musa truncata* colonizing a bared roadside, with two tree ferns, *Cyathea contaminans.* 1500 m elevation, Malaya.

**Fig. 3.9.** A giant *Shorea curtisii.* Note the two men up the tree. Brunei.



**Fig. 3.11.** *Balanophora latisepala* showing a male inflorescence. Lower montane rain forest, Malaya.

Balanophoras are heterotrophs, they have no leaves or chlorophyll and are parasitic on tree roots.

**Fig. 3.12.** *Rafflesia pricei.* Note fly for scale. Sabah, Malaya.

Rafflesias are parasites which live inside the stems of the woody climbing vines *Tetrastigma* from which only the flowers emerge. These are blotched red and white, smell of carrion, and are pollinated by flies.
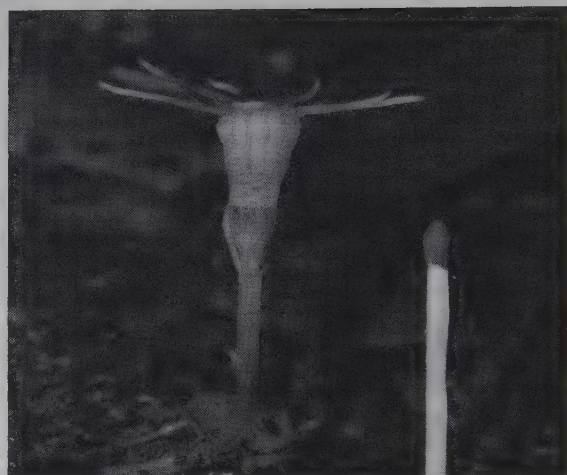


**Fig. 3.13.** *Thismia aseroë.* Tiny saprophytes of the rain forest floor which live on dead plant parts and have only the flowers above ground. Lower montane rain forest, Malaya.

## 3.1. Climbers and epiphytes

There are two different and distinct sorts of climber. Big woody climbers are those that hang freely from trees, for example *Gnetum* (Figs. 3.14, 3.15) with its hooped stem, gnarled *Bauhinia*, and in the Old World, especially Asia, the spiny climbing palms with scaly fruits called rattans. Big woody climbers have their leaves up in the top of the canopy, and some have crowns as big as any tree. They are strongly light-demanding and grow up in canopy gaps besides being abundant on forest fringes. The other kind of climber adheres to the tree trunks by specialized roots and may completely hide the bark beneath (Fig. 3.16). These are called bole climbers. They are especially common in very humid climates and uncommon or rare in forests that experience a strong dry season. Bole climbers are usually mixed with epiphytes and with a group of species called hemi-epiphytes which commence life as bole climbers but become epiphytes by dying off behind; by this curious procedure they slowly climb the trunk of the supporting tree. Bole climbers and epiphytes are zoned (Fig. 3.17), being specialized to the different forest interior microclimates (Fig. 7.1). In the

very humid, dark lower layers shade-dwellers, or skiophytes, occur. Some, for example the filmy ferns, are poikilohydric: they have thin leaves which have the capacity to rehydrate without damage after desiccation. On the upper boles, in the crowns and in canopy gaps photophytes occur (Figs. 3.18–3.22). These are homoiohydric; they resist desiccation by various adaptations. The leaves are leathery with thick cuticles, there may be water-storage organs, e.g. the pseudobulbs of some orchids; and bromeliads, abundant in the neotropics, have leaf bases arranged to enclose a space or tank which collects water. Many photophytes have crassulacean acid metabolism, CAM. Some epiphytes trap nutrients by collecting falling detritus amongst their leaf bases. Humus then develops, and roots push out into it, for example the stag's horn and bird's nest ferns (*Platycerium, Asplenium*: Figs. 3.18, 3.22). Other epiphytes may colonize and 'aerial gardens' form. The numbers of epiphyte species increase with wetness of climate. Counts in forests in northwestern tropical America have found 9–24 species in dry forests and 238–368 species in very wet forests, respec-

**Fig. 3.14.** A big woody climber, *Gnetum* sp. showing the distinctively hooped stem of this genus. Malaya.

Free-hanging big woody climbers like this are a characteristic life-form of many lowland rain forest formations.

tively 2 per cent and 23–24 per cent of the local flora.[66]

On old leaves a film of a special class of epiphytes called epiphylls often grows. These are mostly Cyanobacteria, green algae, bryophytes, lichens or small filmy ferns. They must impair leaf function, and have been shown to do so in coffee plantations.



**Fig. 3.15.** Cauliflory: *Gnetum cuspidatum* with its seeds borne on the stem (note swollen, hooped nodes). Malaya.



**Fig. 3.16.** Bole totally clothed by aroid bole climbers, (probably *Scindapsus* sp.). Big woody climber to right. Sumatra.

**Fig. 3.17.** Bole climbers occur in zones. Lowland rain forest, Kolombangara, Solomon Islands. (Whitmore 1974.)
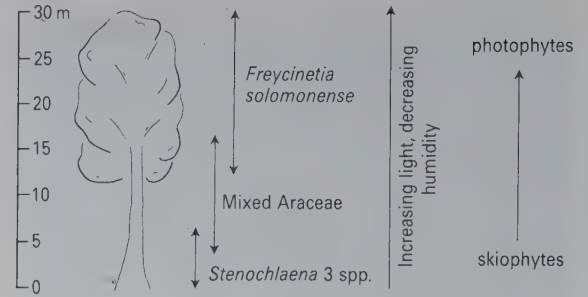


**Fig. 3.18.** *Platycerium*, the stag's horn fern, an epiphyte of tree crowns; on *Campnosperma auriculatum*. Singapore.

This fern has two sorts of fronds, one sort form a nest in which humus collects, the others, the fertile fronds, are pendent and much divided.
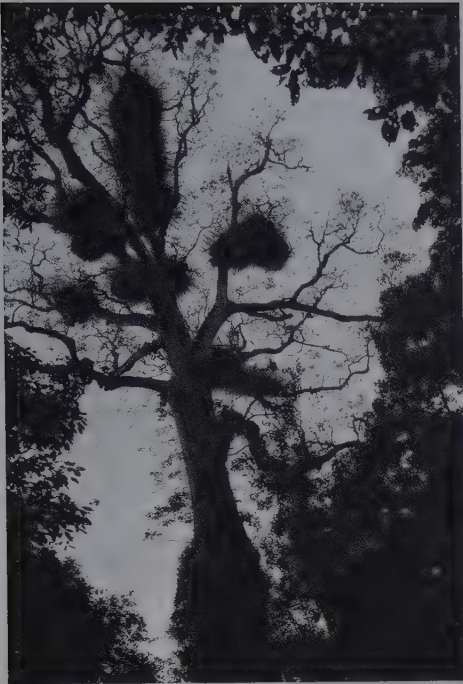
**Fig. 3.19**. *Drynaria sparsisora*, another nest-forming epiphytic fern of tree crowns, forms gigantic masses, seen here in the crown of a *Toona australis* emergent tree flowering after it has shed its leaves. Queensland.



**Fig. 3.20**. Two epiphytic orchids *Maxillaria eburnea* (front) and *Diothonea imbricata* (behind) from the montane rain forests of Guyana. (Lindley's *Sertum Orchidacearum* 1838, plate 40.)

These are photophytic epiphytes of tree crowns. Crown epiphytes live in a periodically hot, dry microclimate and have many xeromorphic features. In these orchids the leaves are thick and leathery and the stems have swollen water-storing leaf bases called pseudobulbs.

**Fig. 3.21**. *Taeniophyllum* is a bizarre genus of Old World epiphytic orchids in which there are no leaves and photosynthesis takes place in green, flattened roots. The name means 'tapeworm leaf'. Malaya.

**Fig. 3.22.** *Asplenium nidus*, bird's nest fern, Old World tropics. Humus collects in the nest-forming frond bases. Java.

## 3.2. Trees

**Crowns**

Crowns have a single leading apical shoot or many, representing monopodial and sympodial construction, respectively. Most trees have monopodial crowns when they are young, many change at maturity. The plant with just an apical tuft of leaves (Fig. 3.7) has the extreme monopodial construction, a form best exhibited by palms (Fig. 6.3). There are no branches just the terminal leaves. In palms the leaf bases conceal the delicate, usually edible, single apical bud and are often spiny or fibrous. Very few palms can resist frost and the family is essentially tropical. If the bud goes, so does the stem: 'like a foolhardy gambler the palm stakes all on a single card'. Many palms grow by a tufting habit, as a result of basal sympodial branching, and this is common amongst Monocotyledons as a whole, as found also for example in gingers, bamboos, and bananas[67] (Figs. 3.1, 3.10). The apical leaf tuft may trap falling detritus, and this has been claimed to provide a source of humus and nutrients for the tree. Other monopodial crowns have lateral branches, and these are often whorled. Where the lateral branches are in tiers the crown has a pagoda-like appearance (Fig. 3.23). In the monopodial juveniles of forest giants the lateral branches are short-lived and eventually fall off. They behave like giant pinnate leaves. In these big trees at maturity, permanent lateral limbs develop (Figs. 2.26, 3.24, 3.28), and on them the juvenile tree form may be repeated—so-called 'reiteration'. The metamorphosis from juvenile to mature form occurs in big trees when the canopy top is reached,[68] presumably triggered by the change in microclimate (Fig. 7.1). Knot-free timber is produced below the sympodial crown. Trees that are tall in virgin forest are usually much shorter where grown as specimens, in arboreta, or in forest regrown on open land.

Tree crowns in fact always have a precise construction,[69] determined by the interaction of three main factors: apical versus lateral growth as just discussed; radially symmetrical versus bilaterally symmetrical lateral meristems; and intermit-

tent versus continuous growth. The construction is most easily observed in juveniles before metamorphosis. Twenty-three different crown 'models' have been recognized. For example, the papaya (*Carica papaya*) has apical growth with lateral inflorescences, is radially symmetrical, and grows continuously. There is little correlation between crown architecture analysed this way and taxonomy; for example Euphorbiaceae have numerous models but Annonaceae and Ebenaceae all have monopodial, radially branched crowns of in-



**Fig. 3.23.** *Fagraea crenulata* has a tiered, pagoda-like crown; Singapore.

Tropical trees have a huge diversity of crown form whose construction has been shown to result from the interaction of three basic processes. Crown form is a valuable aid to species identification, together with bark, buttress, and bole: there is no need to rely on flowers or fruit.

termittent growth. Nor is there any correlation with ecology. The adaptive significance of architectural models is unresolved.

## Leaves

The first impression is of gloomy, dull green, uniform foliage. This is quickly dispelled by closer inspection. There is actually a great diversity in leaf size, shape, nerve-pattern, margin, texture, and colour. Lamina sizes amongst lowland evergreen rain forest trees are mainly but not entirely notophyll and mesophyll (Fig. 3.25), but as was described in Chapter 2 microphylls are predominant in heath and upper montane forests. In lowland rain forests, species with larger leaves are found in the lower part of the canopy where it is most humid and cool and with less water stress.

Pinnately and palmately compound leaves are frequent in lowland rain forest (Figs. 2.5, 3.26). The biggest leaves are found amongst giant monocotyledonous herbs, the aroids (Figs. 1.8, 5.6), gingers and their relatives (Zingiberales), and palms.

Leaves commonly possess drip tips (Fig. 3.27). Recent research has demonstrated these really do hasten drainage of water films, which probably therefore retards the growth of epiphylls, as well as reducing loss of soluble nutrients by leaching.

A flash of colour glimpsed up in the canopy, as seen from the forest floor, or a coloured crown seen looking out over a hillside, is likely to be young leaves not flowers. Before full expansion the leaves of many species are tinged reddish, though they may be white and in a few rare cases are blue. This very striking characteristic of tropi-
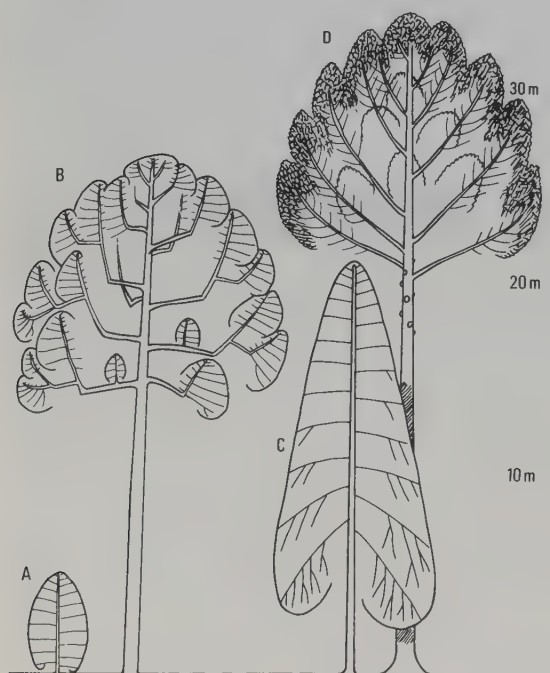


**Fig. 3.24.** Crown construction of two dipterocarps. *Shorea mecistopteryx* (A, B) and *Dryobalanops aromatica* (C, D). (Hallé and Ng 1981, in Whitmore 1984a, Fig. 2.9.)

The juvenile tree (A, C) has monopodial crown structure. At maturity the crown is metamorphosed into a sympodial structure (B, D) which has numerous small subcrowns. In *S. mecistopteryx* these are reiterations of the juvenile tree.
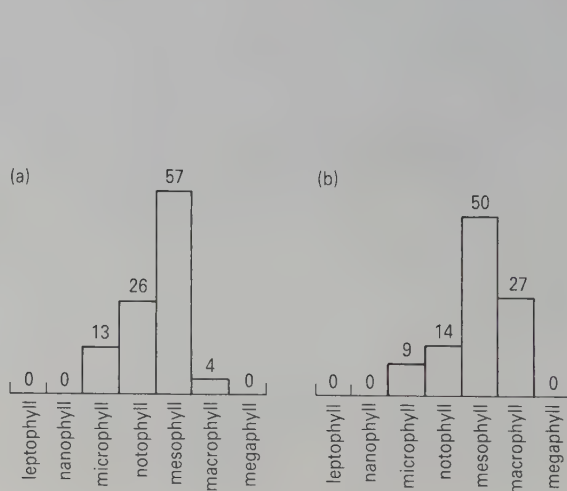


**Fig. 3.25.** Leaf size spectrum. (a) Lower montane rain forest (elevation 1710 m). (b) Lowland rain forest (520 m). Amazonian slope of the Andes in Ecuador. (After Grubb *et al.* 1963, Fig. 5.)

Characteristically, the lowland forest has larger leaves. The leaf size spectrum has proved a useful tool in the analysis of rain forest physiognomy. Here the percentage of species with leaves of different size is shown (sometimes number of individuals is used). The spectrum was proposed by Raunkiaer (1934) and modified by Webb (1959) who introduced notophylls (2025–4500 mm²) for part of the mesophyll class. They should be consulted for further details. Leaf area can be estimated with sufficient accuracy as 2/3 lamina length (to base of drip tip) × breadth.

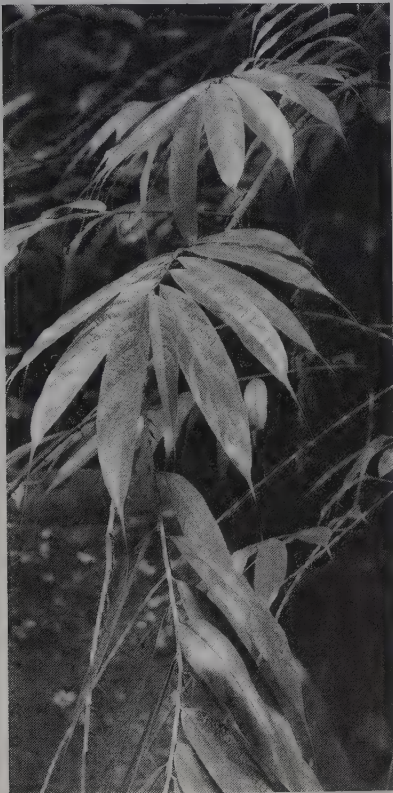**Fig. 3.26**. The giant palmate leaf of *Trevesia cheirantha*, 'Ghost's Footprint'. Malaya.



**Fig. 3.27.** Drip tips of *Ficus beccarii*. Malaya.

cal rain forests still defies scientific explanation. Unlike temperate deciduous forests, there are no spectacular autumn colours in the tropical rain forest. In fact, brightly coloured senescent leaves are sufficiently uncommon to be a useful aid to identification, for example *Elaeocarpus* leaves wither a clear red.

## Boles

The interior of rain forest is often likened to a cathedral with giant columns reaching up to a leafy roof (Figs. 2.24, 3.28). Boles in fact commonly taper slightly, for which foresters make allowance when constructing volume tables. They may be fluted, and occasionally take on a bizarre form (Fig. 3.29).



**Fig. 3.28.** Cylindrical bole of the valuable timber species *Agathis robusta* ssp. *nesophila*. Highlands of Papua New Guinea.

The smooth bark with distant papery scales has scattered whitish microlichens. The big permanent limbs of the mature crown are visible, so are scars left by the temporary branches of the juvenile tree.

**Fig. 3.29**. No one can fail to recognize a mature *Pertusadina* tree because of its totally bizarre latticed trunk. Malaya.



**Fig. 3.30**. Steep plank buttresses of a big kapok tree, *Ceiba pentandra*. Ghana.

Kapok reaches 70 m tall in Africa; this variety (var. *caribaea*) is the tallest rain forest tree in the continent and also occurs in South America (Fig. 1.6) together with the other three species of *Ceiba*. It is likely that *C. pentandra* was dispersed on sea currents to Africa where it now grows wild from Senegal to the Great Rift Valley and Angola. The useful fibre kapok from inside the fruit is derived from a small spineless variety (var. *pentandra*) which is cultivated throughout the tropics (Fig. 10.4).

## Buttresses

Buttresses (Figs. 3.30, 3.31) are prominent in some forest formations. They differ in shape, size, and thickness between species and families; for example they are particularly marked in Bombacaceae. Buttresses are tension structures, resonating when struck with an axe, and are mainly found on uphill sides of trees and counterbalancing asymmetric or epiphyte laden crowns. An analysis of the stresses to which a tree is subject and the strength of its wood shows buttresses are indeed of structural importance, helping to support the tree.[70] Flying buttresses occur in some families (Fig. 3.32), and are common in swamp forests. Stilt roots are another feature. They are very characteristic of pandans, and are also found in palms, some mangroves (Fig. 2.14), and a few other trees.

## Bark

Bark is extremely diverse.[71] Colour varies from coal black in ebony (*Diospyros*) and some Myristicaceae to white in *Tristaniopsis*,[72] through bright rufous brown (*Eugenia*). *Calycophyllum* of the neotropics has bark like burnished copper. The bark surface may be smooth, scaly, fissured, scrolled, or dippled (Figs. 1.4, 2.26, 2.31, 3.28). Smooth barks have a long persistent surface and

**Fig. 3.31.** Bombacaceae are characterized by particularly huge buttresses, which attain Brobdingnagian size in *Huberodendron duckei*. Brazilian Amazon.



**Fig. 3.32.** Flying buttresses and stilt roots of *Uapaca guineensis*. Ghana.

these often house lichens which may be specific, e.g. *Disopyros* commonly has a dark green micro-lichen. The bark may contain a latex, resin, or coloured sap.

The botanist, confused by Jacobs' cacaphony of fallen leaves, uses the crown, bole, buttresses, and bark to help him with identification. Flowers are seldom present and are hard to see or to examine high in the canopy but the characters of the living tree are so diverse they provide ample clues for identification. The most useful forest Floras are based on these 'field' characters and use them entirely for their keys.[73]

## Roots

These are, for obvious reasons, less well known than the parts above the ground. Some rain forest species have a deep tap root. Others have 'sinkers', roots that descend vertically from spreading roots or buttresses. Most of the root biomass is in the top 0.3 m or so of the soil and there is sometimes a concentration or root mat at the surface. The relatively few deeper roots may be important in gathering nutrients from decomposing rock or which have leached down; species with such roots have potentially an important role in low-input sustainable agriculture based on tree and crop mixtures (p. 144). Fine roots are difficult to study; it is hard to extract them from the soil and when extracted to see which are alive. Roots up to 2 mm in diameter form 20–50 per cent of the total root biomass[74] and their believed rapid turnover is probably a significant part of ecosystem nutrient cycles (Chapter 8).

It has recently been realized that, as in other forests, in the rain forest nearly all trees have

mycorrhiza. These are mainly endotrophic, vesicular arbuscular in type, but a few groups, some very important (Dipterocarpaceae, Fagaceae, *Eucalyptus*, Leguminosae/Caesalpinoideae), have

ectotrophic mycorrhiza. Nitrogen-fixing nodules occur in most Leguminosae (the bacterium *Rhizobium*), and *Alnus* and *Casuarina* (the fungus *Frankia*).

## 3.3. Seasonal rhythms

### Shoot and leaf growth[75]

Tropical rain forests are evergreen and the climate is benign to plant life, always warm, and moist for all or most of the time. One might expect growth to be continuous. A few trees and other plants have indeed been found to grow all the time, as measured by production of nodes, each bearing one or a few leaves. The pioneer tree *Macaranga tanarius* is an example (Fig. 3.33). Internode elongation rate, another measure of growth, is constant in this species but in trees of other species, despite continuous production of nodes at a steady rate, elongation rate, and hence height growth rate, increases through time (Fig. 3.34). The exact measure used for growth matters; even with *Macaranga tanarius* we do not know if meris-

tem activity is continuous. Palms exhibit continuous growth and the hoop-like leaf scars left on the trunk show elongation is also steady, though stem diameter waxes and wanes with growth conditions (Fig. 3.35).

Most rain forest trees, however, exhibit intermittent shoot growth (Fig. 3.36). A number of nodes form with their associated flush of new leaves, sometimes brightly coloured at first, and often as pendent, hanging tassels; followed by a resting period. The intermittent growth of the shoot tips is seldom reflected by growth rings in the wood, and where it is these are not annual and often not annular either. Rain forest trees, unlike those of seasonal climates, cannot be aged by
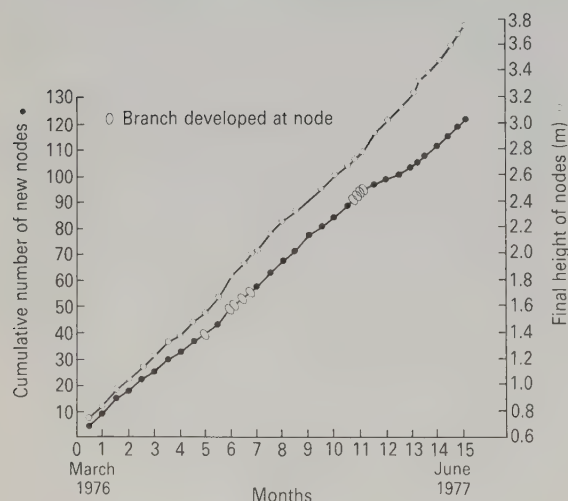


**Fig. 3.33.** In *Macaranga tanarius* height growth is steady. New nodes form continuously and regularly and every internode elongates by the same amount. (After Ng 1984, Fig. 3).
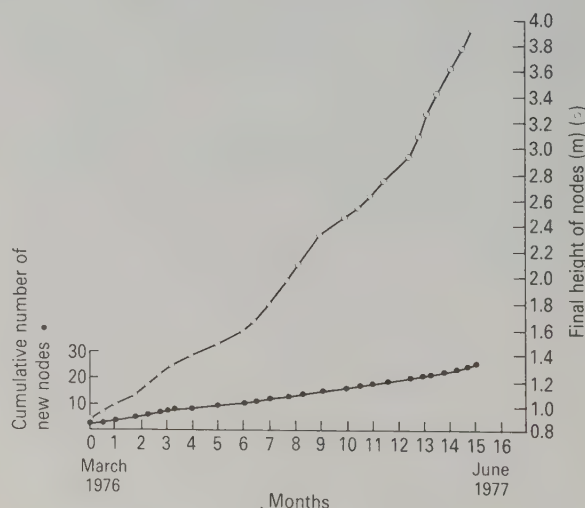


**Fig. 3.34.** In *Oroxylum indicum* height growth increases through time. New nodes form continuously and regularly (cf. Fig. 3.33) but the internodes continue to elongate. Growth rate measured by node production is linear but measured by height it accelerates. (After Ng 1984, Fig. 5.)

Fig. 3.35. This old flowering *Corypha umbraculifera* (talipot palm) in the strongly seasonal climate of east Java has experienced good and bad growing periods.
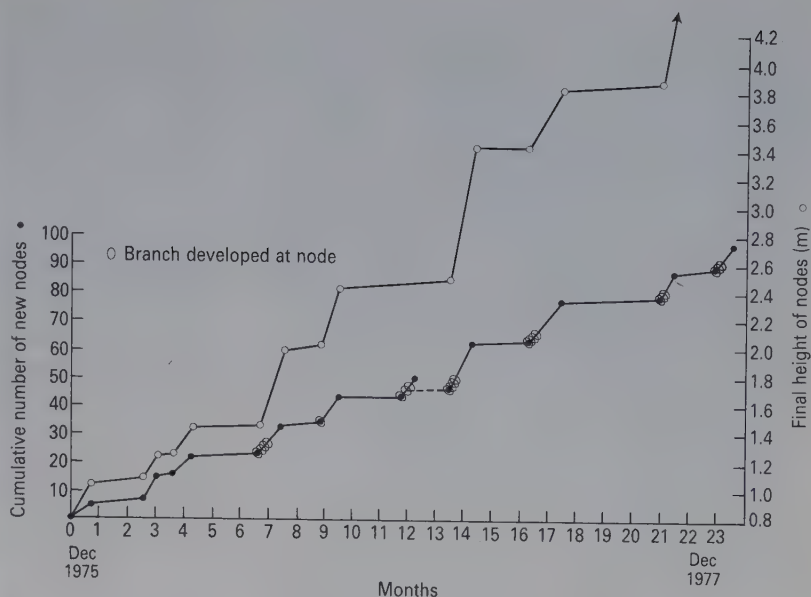
**Fig. 3.36.** In *Harpullia confusa* height growth is in flushes. New nodes form intermittently with resting periods between. The internodes continue to elongate after initial formation. (After Ng 1984, Fig. 10.)

counting wood rings (section 7.8).

Intermittent growth inhibits the build-up of fungi or insects which attack young leaves. In Malaya young leaves of *Hevea* are often attacked by two fungi, a mite, and a thrip any of which occasionally causes defoliation, even though the tree produces leaves in flushes.

In a study of 81 species of dipterocarps at Kepong, Malaya, 70 produced leaves in flushes and in the nearby Ulu Gombak forest 38 out of 41 species flushed.

## Leaf fall[76]

The sharp distinction between deciduous and evergreen species of temperate climates does not exist in the humid tropics.

Trees with continuously growing shoots suffer continuous leaf fall. Leaf life span varies from about 3 to 15 months. A young palm may accumulate leaves and develop an oblong crown (Fig. 6.3), but at maturity for every new leaf unfurled, an old one drops off.

Amongst the majority of species that grow in flushes we may distinguish three patterns of leaf fall. Where leaves are shed well before bud-break the crown will be bare for a period, perhaps only a few days. Such trees are termed deciduous. In the humid tropics such species flower on the bare crown, for example *Bombax*, *Firmiana*, *Pterocymbium*, and *Toona* (Fig. 3.19), whose bird pollinators are probably assisted by the lack of leaves.

In other species leaf fall occurs at about the same time as bud-break (Fig. 3.37), but may be a few days earlier or later, depending on particular weather conditions or on the local climate. For example the rain tree (*Samanea saman*) is evergreen in Singapore, but is bare for a few days in central America where it is native. In Singapore it briefly has two coexistent leaf flushes and in America it is briefly deciduous. Species with this behaviour are called leaf exchangers. The gardener whose task is to sweep up the fallen leaves only has to do so once or twice a year.

**Fig. 3.37**. *Dyera costulata* (jelutong) is a
leaf-exchanging species. On this tree a flush of new
leaves is seen. The new leaves are expanding
immediately after the old ones were shed. Note
*Platycerium* crown epiphytes. Malaya.

Finally, leaf fall may occur well after bud-
break. Species with this pattern are evergreen.
Leaves live about 7 to 15 months and leaves of
several flushes sometimes occur together. In
young trees of the dipterocarp *Neobalanocarpus
heimii* up to seven leaf generations have been
found to be present simultaneously.

## Synchronization

Leaf life spans on isolated relict and planted speci-
men trees observed in Singapore at the tip of the
Malay Peninsula were found to be 12 months in
four species and 6 months in another three
species.[77] One might adduce a climatic trigger for
leaf fall except that 17 further species had life
spans with no relation to the year, and were more
or less constant in each species but with individual
trees out of phase. This suggests there is a genetic-
ally determined life span; leaves become old and
less efficient as they become more shaded and
accumulate epiphylls and are eventually dropped.

These specimen trees all behaved as indi-
viduals. A few species showed lack of synchrony
within the crown between different limbs—
mango (*Mangifera*) is a good example—and this
has been called 'manifold growth'. It was not until
a study was made of trees in their natural habitat
that it was realized that even in the almost aseasonal
climate of Malaya (Fig. 2.1) there is an annual
rhythm in phenology. The study covered 9 years
at the Ulu Gombak[78] forest and 61 trees of 46
species were observed monthly from a platform in
the crown of an emergent. There were two leaf
flushes per year, in February to April, and in Sep-
tember to October. Most leaf change occurred
then, though different individuals of a species
were often not in exact synchrony. The main peak
of leaf growth came after the driest time of year,
the second lesser peak began before but extended
into the wettest time of year. Most trees flowered
annually, mainly at the early leaf flush, but some
at the later one. The Dipterocarpaceae however
only flowered twice, in years which also saw
heaviest flowering of the other trees. It is well
known in Malaya that durians and other forest
fruits are on sale twice a year, and there are spor-
adic bumper harvests.

In more strongly seasonal tropical climates than
Malaya there are more numerous deciduous spe-
cies. Crowns are bare in the dry season, but flower-
ing and leaf flushing show complex patterns that
are not all easily relatable to climatic seasonality.
An interesting study in the tropical seasonal forest
at Guanacaste, Costa Rica,[79] found that flushing
and flowering were controlled by tree water status,
which was monitored by measuring trunk girth
very accurately with dendrometers. On dry sites
leaves were lost early in the dry season. In most
species rehydration and bud break occurred fol-
lowing heavy rain, but in a few leaf loss allowed
rehydration and was followed by bud break,
sometimes with flowering, without rain having
fallen. On wet sites the species remained ever-
green or just exchanged their leaves. It remains to
be seen how common this mode of control is.
There are certainly forests where it does not oper-
ate, for example most species in the dry deciduous
dipterocarp forests in Thailand produce new
leaves more or less synchronously before the first

rains break the annual 4–5 month drought. Here the trigger to flush has yet to be discovered.[80]

## Flowering patterns

Climax species in rain forests mostly flower once a year and at about the same time. Some figs (*Ficus*) become fertile very irregularly in contradiction to this generalization, and with important consequences for their dispersers (section 4.3). There have been suggestions, which remain unsubstantiated, that small trees within the canopy flower more continually. By contrast, pioneer species, and hence secondary forests, are in continual flower, some species several times a year and others all the time (e.g. in Asia *Adinandra dumosa*, *Macaranga heynei*, and *Dillenia suffruticosa* and in Africa *Vernonia conferta* and *Trema orientalis*).

*Monocarpy*. A few species, mostly monocotyledonous plants such as some palms and bamboos, exhibit monocarpic or 'big bang' flowering. Usually the plants grow for many years and then over a whole district simultaneously flower, fruit, and die. This is best developed in the seasonal tropics, for example many bamboos in continental Asia, including China, whose copious fruitfall is followed by plagues of rats, and then a dearth of materials for house construction until fresh clumps grow up. One of botany's mysteries is how subdivisions of a single bamboo clump grown apart time themselves to flower simultaneously. One striking example concerns *Arundinaria falcata* which flowered 35 years after introduction from India in Algeria, France, Luxembourg, and Ireland.[81] Most spectacular of all monocarpic species is the Talipot palm (*Corypha umbraculifera*), which grows the largest inflorescence in the world (Figs. 3.35, 3.38): a gigantic apical candelabrum, which then develops hundreds of thousands of fruits before the palm dies. A whole avenue of talipot at the Peradeniya Botanic Garden, Sri Lanka flowered and then died simultaneously.

There are fewer monocarpic woody dicotyledonous plants. The shrub *Strobilanthes* with several species through the Asian rain forests is one. *Tachigali*, with 24 species through the neotropics, *Harmsiopanax ingens* in the mountains of

New Guinea,[82] and *Cerberiopsis* (3 spp., New Caledonia) are the only trees so far known which have this habit.

*Mass flowering in western Malesia*. Every year in Malaya and Borneo there is a single period of heavy flowering and fruiting. As described above, careful studies over 9 years at Ulu Gombak, Malaya, showed there is a second lesser episode and that production of new leaves also occurs mainly at these times. These two annual events coincide with two slightly drier periods, a few weeks of little rain. Once or twice a decade the early dry spell is unusually strong and is followed by heavier than usual flowering and fruiting, and in these years there is gregarious heavy flowering and fruiting of Dipterocarpaceae (Fig. 3.39).

Different species of dipterocarp flower after each other over a period of several weeks but fruiting is simultaneous, at about the time heavy rains begin. The fruits are highly favoured by pigs and mass fruiting is believed to satiate these predators as well as seed-attacking beetles. There is strong selection pressure against any tree out of phase, so mass fruiting is a self-reinforcing phenomenon. However, mass fruiting in this family is confined to the west Malesian rain forest species, and we have no explanation as to why the gregarious dipterocarp *Anisoptera thurifera* of New Guinea flowers and fruits every year.

There are no other tropical rain forest plants that show such massive occasional fertility. It is this property that makes dipterocarps and the rain forests they dominate unique (see section 7.7).

## Triggers for flowering

Chilling of already formed young flower buds, triggering them to complete their development, has long been known to be the flowering stimulus for some species.[83] For example *Zephyranthes rosea*, the rain lily, flowers after the stimulus of rain and associated cooling; some orchids and trees (e.g. the pigeon orchid *Dendrobium crumenatum*, a common epiphyte of wayside trees of Malaya and the angsana tree *Pterocarpus indicus*) burst into bloom some days after a midday storm causes sudden chilling.

**Fig. 3.38.** *Corypha umbraculifera*, the giant talipot palm, is monocarpic. It flowers once and then dies. Malaya.

An early European traveller wrote back from India in 1681 'one single leaf (is) so broad that it will cover some fifteen to twenty men, and keep them dry when it rains'.
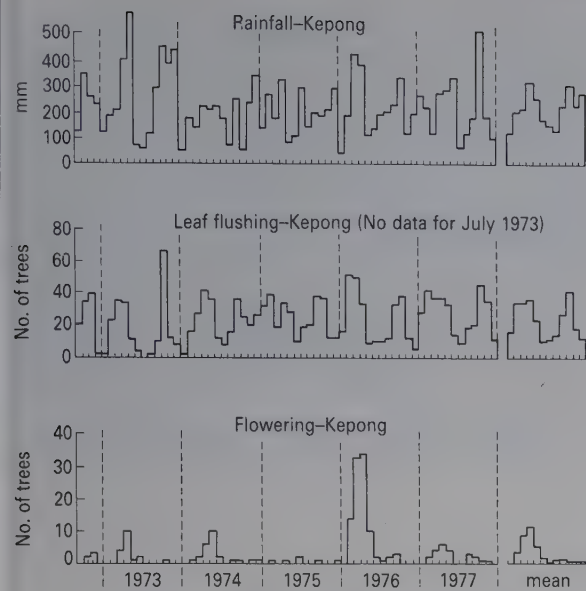
Dipterocarpaceae may show some such trigger. As mentioned above mass flowerings coincide with exceptionally dry weather. Up to about half of all dipterocarp trees burst into flower simultaneously. Later, the corollas carpet the ground like fallen, tinted confetti and are followed after 3–4 months by a heavy fruit fall. There has been much speculation as to the exact nature of the trigger. Drought, or an increase in hours of bright sunshine, or an unusually big difference between night and day temperatures because of the cloudless weather occurring at that season, have all been suggested. The problem has still not been finally resolved.[84]

**Fig. 3.39.** Leaf flushing and flowering of dipterocarps, and rainfall. Kepong, Malaya. (After Ng 1984, Fig. 12).

## 3.4. Plant life—Chapter summary

1. There is a great richness of life forms in tropical rain forests. The trees provide support for climbers and epiphytes. There are species of all life forms adapted to the different forest interior microclimates; the broadest classification is into photophytes and skiophytes.

2. The first impression of a uniform phalanx of trees is quickly dispelled. There is enormous variety in crown, bole, buttresses, bark, roots, and leaves. Flowers are ephemeral and species are usually identified from these characters of the living tree.

3. Only a few species grow continuously. For most, shoot and leaf growth is intermittent, in flushes. Young leaves are commonly highly coloured. Leaf fall follows various patterns, and often occurs after a new flush has grown, but there may be a bare period and this is more pronounced in seasonal climates.

4. Forests show synchronized leaf flushing, and usually bear flower and fruit annually. West Malesian rain forest Dipterocarpaceae are unique in their gregarious flowering and fruiting only a few times a decade.

5. Pioneer species flower more continually.

6. A few species, especially in seasonal forests, are monocarpic, flowering then dying.

7. Triggers to flowering include low night temperature and the chilling of bud initials early in their development.

# 4

# Rain forest animals[85]

Animal life is, on the whole far more abundant and varied within the tropics than in any other part of the globe, and a great number of peculiar forms are found there which never extend into temperate regions. Endless eccentricities of form and extreme richness of colour are its most prominent features, and these are manifested in the highest degree in those equatorial lands where vegetation acquires its greatest beauty and fullest development.

A. R. Wallace *Tropical nature and other essays*, 1878.

## 4.1. Richness and diversity of animals

The casual visitor entering a rain forest is overwhelmed by the lush diversity of the plants but disappointed by the apparent absence of animals, except for the rising and falling resonant trill of cicadas, and very soon too by the attentions of biting insects, and in the Eastern tropics of blood-sucking leeches. The observant naturalist however, detects the signs of bigger animals. In Borneo for instance he may notice an orang utan's nocturnal sleeping platform of branches roughly thrown together high in the canopy; scratches on a tree trunk where a big cat has sharpened its claws or where a sun bear has tried to break into a bees' nest; part of the forest floor swept clean of leaf litter as the display ground of an argus pheasant; the muddy hollows or disturbed soil surface of wallowing or rootling pigs. To see the animals and not just their signs he will walk quietly through the forest at dawn or dusk when birds are most active, or at night when many mammals and frogs are awake and can be seen in the light of a headlamp.

Tropical rain forests are indeed fabulously rich in animal life as A. R. Wallace and the other nineteenth century naturalist explorers reported. Just how many species the world's rain forests contain is still, a century after their pioneering studies, only a matter of rough conjecture. For mammals, birds, and other larger animals there are roughly twice as many species in tropical regions as temperate ones (Fig. 4.1). These groups are fairly well studied, insects and other invertebrates much less so, and if the same proportion between temperate and tropical species holds for them then the tropics as a whole may hold a total of 2–3 million animal species; the great majority of these are undescribed insects, with their greatest abundance in rain forests.

The richness of various animal groups in different patches of rain forest is shown in Table 4.1. The counts of birds and of amphibians (frogs and toads) at the two Ecuadorian sites are probably world records, as are the discovery of 550 species of butterflies at Ega in the Amazon by Bates last century, and of a single tree at Tambopata, Peru, with 43 ant species in 26 genera—about the same number as the whole British Isles or Canada.

The question of how many species live in the world's tropical rain forests is currently under debate, as part of the concern for their adequate conservation to be discussed in Chapter 10. The huge figure of 2–3 million species, or two-thirds of all forms of life on earth, may even, perhaps, be a substantial underestimate. T. L. Erwin[86] has argued that the global total count may be nearer 30 million species, based on his analysis of the insects living in the crown of *Luehea seemannii* in a scrubby tropical seasonal forest in Panama. Nineteen trees, sampled over three seasons, yielded 955 species of beetles not counting weevils. They
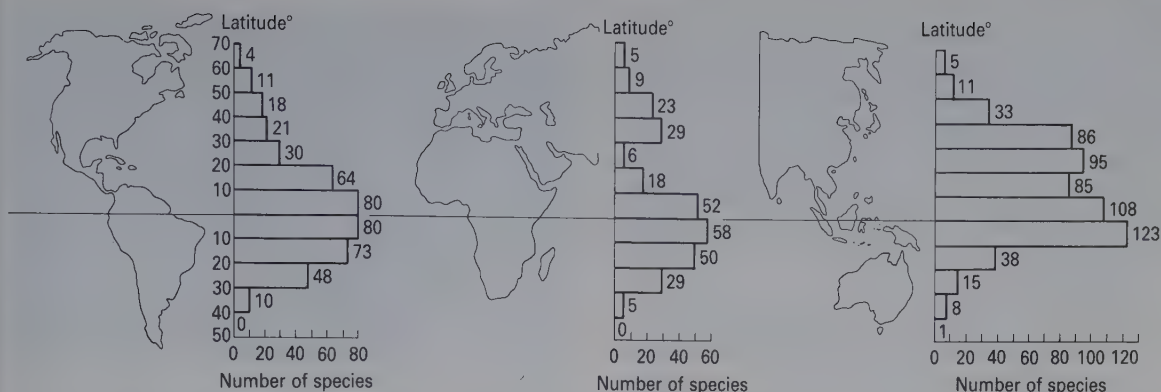
**Fig. 4.1.** Decrease away from the tropics in species numbers of swallowtail butterflies exemplifies a very common biogeographic pattern. (Collins and Morris 1985, Fig. 2, in Longman and Jenik 1987.)

Table 4.1

*Species richness of various groups in some well-studied lowland rain forests*

| | Area (km$^2$) | Mammals (primates) | Birds | Number of species Reptiles | Amphibians | Moths | Vascular plants |
|---|---|---|---|---|---|---|---|
| Neotropics: | | | | | | | |
| Panama | | | | | | | |
| Barro Colorado Is. | 15 | 97(5) | 366 | 68 | 32 | – | 1369 |
| Costa Rica | | | | | | | |
| La Selva | *c.* 15 | *c.* 100(3) | >400 | >50 | 41 | *c.* 4000 | 2200 |
| Ecuador | | | | | | | |
| Limoncocha | 15 | – | 480 | – | – | – | – |
| Santa Cecilia | 3 | – | – | – | 81 | – | – |
| Africa: | | | | | | | |
| Gabon | | | | | | | |
| Makoukou | 2000 | 199(14) | 342 | 63 | 38 | – | – |
| Far East: | | | | | | | |
| Malaysia | | | | | | | |
| Pasoh | 8 | 89(5) | 212 | >20 | 25 | – | – |
| Papua New Guinea | | | | | | | |
| Gogol | 10 | 27(10) | 162 | 34 | 23 | – | – |

Various sources                    –, no data available

were extracted by fogging the tree crowns with knockdown insecticides. Erwin's study breaks away from earlier loose arguments about species numbers by providing a new focused approach, and although one might disagree with the steps in his extrapolation he shows the way objective estimates can be obtained.[87]

Taxonomic description, mainly of vertebrates, has proceeded further than ecological studies, and investigations on the ecology of animals in rain forests have developed more recently than of plants. In this chapter something is said about the differences in vertebrate communities from place to place, followed by discussion of the main means

whereby so many species are able to coexist, and then on what factors may limit animal numbers. In Chapter 5 we go on to describe interactions between animals and plants, cohabiting components of the rain forest ecosystem. Invertebrates are important as decomposers of dead organic matter on the forest floor and this subject is discussed further in section 8.2.

Differences and similarities can be seen between the faunas of the three tropical regions. Let us consider primates as an example. In tropical America and parts of Africa up to 14 sympatric primate species coexist, but there are nowhere more than 9 in the Asian forests. Primate biomass is highest in African rain forests where it may reach over 2000 kg km$^{-2}$. In Africa, and also in Asia, there are numerous species specializing in eating leaves (folivores) which they are able to digest using commensal bacteria that inhabit modified, extended parts of the gut. America has a larger number of frugivore-insectivore species than elsewhere, none which are so dependent on leaves, and some species which are much smaller than are found elsewhere.[88] In both Africa and America mixed-species primate troops occur, but none have been found in Asia. The proportions of primates to other fruit- and leaf-eating canopy-dwellers varies from place to place. New Guinea has more frugivorous birds than elsewhere because there is only one competing mammal, a tree-kangaroo, and no primates or squirrels. Within tropical America it has been suggested that the unusually high density of sloths (2130 kg km$^{-2}$) on Barro Colorado Island, may explain, by competition for food, why howler monkeys are unusually sparse.[89]

South America is sometimes called the bird continent. It has a particularly rich bird fauna, followed by Asia, with Africa trailing behind. In the Old World tropics hornbills (Fig. 4.2) form a guild of specialist canopy-top frugivores. This niche is filled in America by toucans, slightly smaller in size but with similar beak construction, which evolved convergently to feed on the same sorts of fruit (section 5.2). Tropical America is also much the richest region in bats, and the Amazon has about half all known species of freshwater fish.



**Fig. 4.2.** Rhinoceros hornbill (*Buceros rhinoceros*). Hornbills are specialist frugivores of Old World tropical forests.

For many rain forest vertebrates fruits are an important component of the diet. This differs from the situation in tropical savannas where herbivores predominate and occur at higher biomass. For example, at the Cocha Cashu rain forest in Peru, mammal and bird biomass was *c.* 2 tonne km$^{-2}$, whereas it can reach 12 tonne km$^{-2}$ in African savanna. Fruits are variously supplemented by other foods. For example, frugivorous birds augment their diet with insects, which are richer in protein, especially during the nesting and moulting season.

Besides differences between the three tropical regions there are other differences within them. One major pattern is that within the African and American rain forests there are areas of especially high species richness, set like islands in a sea of relative poverty. This is shown well by African birds and is paralleled in America by many groups, including birds and butterflies (Figs. 6.16, 6.17). No such patchiness has been detected in Asia where the major pattern is set by Wallace's Line, one of the sharpest zoogeographical boundaries in the world and which delimits the continental Asian faunas from the Australasian (Fig. 6.5). These patterns are now realized to have explanations based on Earth history as will be discussed in Chapter 6.

Finally, in all parts of the tropics there is a general diminution in species number with increasing elevation, from lowland to montane forest (Fig. 4.3).

## 4.2. Modes of coexistence

Studies have now been made in many parts of the tropics to elucidate how so many animals coexist in the same forest. They do so by specialization. Rain forest is lofty and provides a diverse three-dimensional living space and a huge variety of foods.

### Specialization in time and space

Some animals are active by day and others by night, and many species live mainly in a single layer of the canopy. Figure 4.4 shows this vividly for the mammals in a rain forest in Borneo. The canopy layers occupied by the different birds at La Selva, Costa Rica, are shown in Table 4.2 and by nine sympatric squirrels at M'Passa, Gabon, in Fig. 4.5. Invertebrates have also developed particular niches in time and space. D. H. Murphy
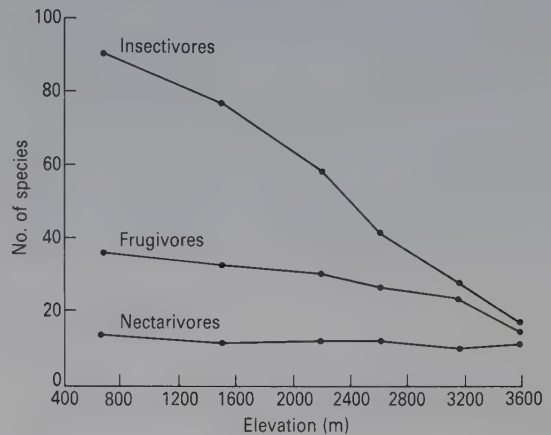


**Fig. 4.3.** Reduction in bird species numbers of three feeding guilds with increasing elevation. Peruvian Andes. (Data of Terborgh in Bourlière 1983.)
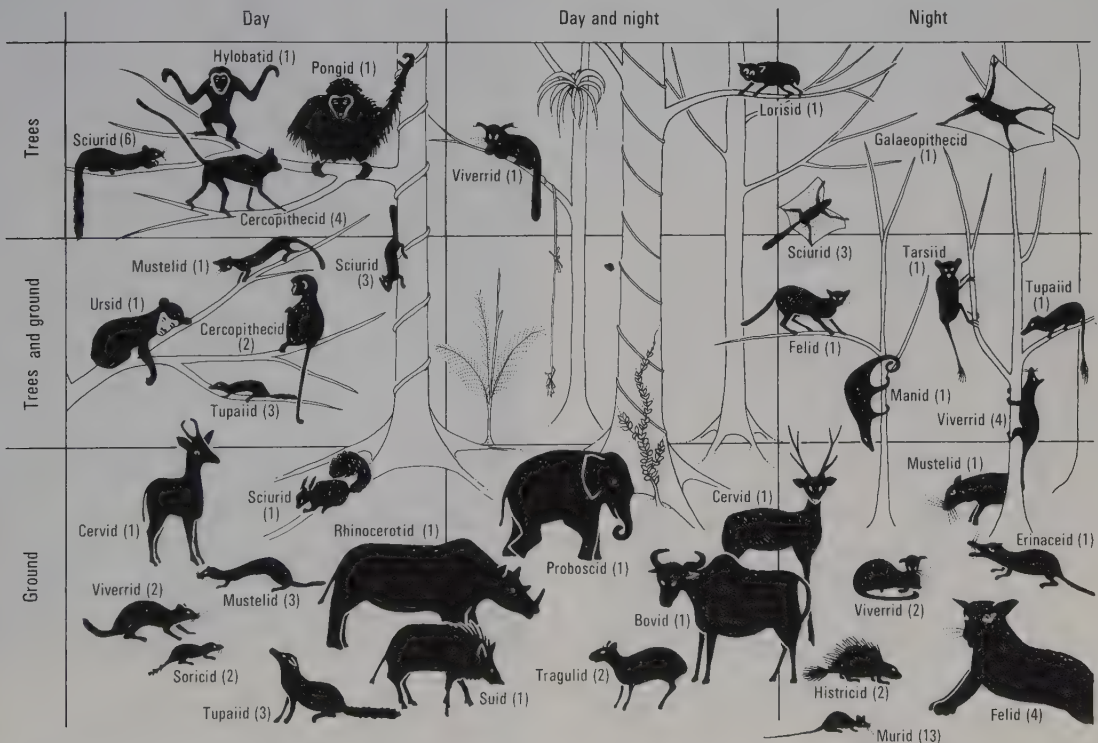


**Fig. 4.4.** Space- and time-partitioning of non-flying mammals in the lowland rain forest of Sabah. (Data of MacKinnon in Whitmore 1984*a*, Fig. 3.1.)

has described how at the Bukit Timah forest, Singapore, there are morning and evening rush hours when cryptozoans move from the soil to feed in the canopy and back, awaited at the foot of the trees by a predatory scorpion, frog, and spider, while during the day these dawn and dusk predators are replaced by others, including a flying lizard. Murphy has also discovered that insects do not fly at random through the forest canopy but follow particular, preferred flight paths, and that along these are concentrated the web-making spiders which prey on them.

The water-filled tanks of epiphytic bromeliads are a particularly special niche in the neotropics (Fig. 4.6). They are veritable aerial aquaria. In Jamaica 68 species have been found to inhabit them, including mosquito larvae. In fact, malaria-control in the New World, unlike the Old, can never be by the elimination of stagnant water because of the presence of these water-tank epiphytes.

The pitcher plants *Nepenthes* of Madagascar, Seychelles, and the Eastern tropics provide another special niche for animals (Fig. 4.7). In Malaya 55 insect species have been recorded as inhabitants of the pitchers, two-thirds of which live and breed there. Amongst the more surprising occasional inhabitants of both bromeliad tanks and *Nepenthes* pitchers are species of freshwater crab.

Table 4.2

*Bird zonation at La Selva forest, Costa Rica*

| | |
|---|---|
| Above canopy | Vultures, hawks, swifts |
| Canopy top | Toucans, cotingas, parrots, cacique birds |
| 15–25 m | Woodpeckers, woodhewers, large trogons, jacamars, puffbirds |
| Understorey | Most hummingbirds, antbirds, manakins, flycatchers, tanagers |
| Forest floor | Tinamous, great curassow, ground doves, wrens |

Data of Slud in Bourlière (1983)
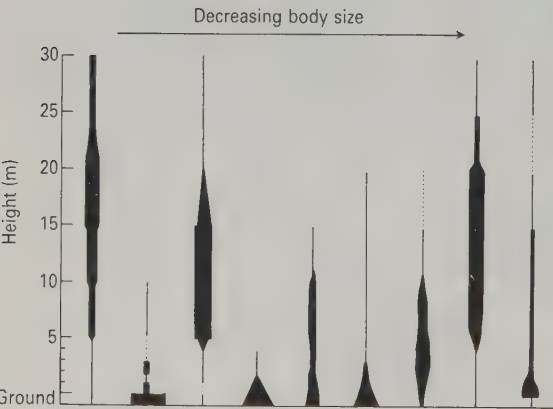


**Fig. 4.5.** Canopy height preferences of nine sympatric squirrel species in lowland rain forest, Gabon. (Data of Emmons in Bourlière 1983).

Note how similar heights in the canopy are occupied by squirrels of very different body weight.



**Fig. 4.6.** Epiphytic bromeliads are a very distinctive feature of the neotropics. Amazonian Ecuador.

Water collects in tanks at the overlapping leaf bases and is absorbed by the plant. This pool provides home for many animalcules, including mosquito larvae.

**Fig. 4.7.** *Nepenthes sanguinea*, Malaya.
These pitcher plants are a feature of the Eastern tropics. Small invertebrates, which fall into the pitcher, drown and are digested by the plant.

## Food preferences

Many cases have now been analysed which show how the animal inhabitants have evolved to share out the food resources of a forest.

Neotropical bats are by far the most complex assemblages anywhere in the world of sympatric mammals, with 35–50 species coexisting in a few square kilometres of forest. Amongst the 35 sympatric species of Barro Colorado Island, Panama, nine food-defined guilds can be distinguished (Table 4.3), each with from one to nine species. Within each guild there is specialization mainly for size of food particle, which is itself proportional to body weight.

In northeast Gabon in Central Africa there are five sympatric nocturnal species of lorises (prosimian primates), a potto (*Perodictus potto*), three bush-babies (*Galago alleni*, *G. demidovii*, *Euoticus elegantulus*), and an angwantibo (*Arctocebus calabarensis*). These avoid competition by partitioning both food and space. In the canopy *G. demidovii* is mainly insectivorous, the potto mainly eats fruits, and *Euticus* feeds on plant gums. The two other species inhabit the undergrowth being mainly frugivorous (*G. alleni*) and insectivorous (the angwantibo), respectively. There are additional differences in hunting technique, with specialization on slow- or fast-moving insects.

Amongst sympatric primates diet is always related to body size. The smallest species are insectivores, but insects cannot supply enough nutrition for medium-sized animals in relation to the hunting effort, and fruit is the most important sort of food. For the largest species leaves and seeds are most important and they also eat some fruit. This is well exemplified at Cocha Cashu described below.

## Breeding sites

Another way species may live together is demonstrated by the extremely rich frog and toad community of a forest at Santa Cecilia in Amazonian Ecuador, now unfortunately destroyed. There the 74 species, all living within 3 km$^2$, were mainly opportunistic feeders and differed mainly by a wide diversity of breeding sites. Ten modes of egg-laying behaviour were distinguished, including deposition in water, on vegetation, in tree cavities, in a depression in the soil made by the male, in foam nests, and on the back of the female. There was also some temporal division, only ten or fewer species being found to breed simultaneously.

Table 4.3
*The nine feeding guilds found amongst the 35 bat species at Barro Colorado Island, Panama*

| 1 | Frugivores | In canopy |
|---|---|---|
| 2 | | Near the ground |
| 3 | | As scavengers |
| 4 | Omnivores | Feeding on nectar, pollen, fruit, and insects |
| 5 | Sanguivores | The vampires, feeding on blood |
| 6 | Carnivores | (Which glean) |
| 7 | Piscivores | (Fish eaters) |
| 8 | Insectivores | Slow-flying hawking |
| 9 | | Fast-flying hawking |

Data of Barrocorso in Bourlière 1983

## 4.3. Carrying capacity of the forest

Ultimately, by whatever manner the animals have evolved to coexist within a particular forest, their numbers are limited by the amount of food available.

Data have been gathered from several rain forests which show how there are periodic lean periods when animals may go hungry. The Cocha Cashu area of the Manu National Park in Amazonian Peru may be used by way of example to show how animals subdivide the resources of the forest and cope with hungry periods.[90] At Cocha Cashu the dominant mammals and birds are frugivores, contributing about three-quarters of the total vertebrate biomass. Amongst the mammals, primates then rodents and peccary are commonest. Fruit production was estimated to be 2 tonnes ha$^{-1}$ year$^{-1}$, but with a 3 month lean period, May to July, when abundance fell to between 2 and 5 per cent of its peak quantities. During the lean period frugivores are forced either to migrate or to alter their diet. Five of the eleven primate species were studied in detail. These were found to shift to different foods and what they ate depended on their size. The two largest species, the capuchin monkeys (*Cebus albifrons*, *C. apella*; 3000–5000 g) concentrate on palm nuts which they are able to crack with their strong jaws, but only the larger species is really strong enough. The squirrel monkey (*Saimiri sciureus*; 800–1200 g) eats figs, but sometimes goes a week with no food or just insects, using up more energy than it gains. The two tiniest species, the tamarins (*Saguinus fuscicollis*, *S. imperator*; 400–500 g) were observed to spend 90 per cent of their feeding time sipping nectar. Only about 1 per cent of the 2000 tree species in the area fruit during the lean period, and these are essential to sustain the frugivorous animals.

There is evidence that palms and figs also play an important role as famine foods in other South American forests. Such plants have been called keystone species because of their vital function. They have obvious importance in forest conservation, and we shall discuss them further in section 10.8.

**Figs as keystone species**

The bustling activity at a large fig is one of the unforgettable spectacles of the [Cocha Cashu] forest. Monkey troops arrive from all directions as if guided by some mysterious perception. We have seen over 100 monkeys of five species and 20 to 30 species of birds feeding simultaneously in a single *Ficus perforata*. How is it possible that so many animals independently discover a tree almost the first day the fruit ripens? We believe they are summoned by the shrill din of the myriads of parakeets (*Brotogerus* spp.) that quickly converge on the scene. These birds are fig specialists as much as *Saimiri*, and the sound of them in numbers is almost certain indication of a fruiting tree.[91]

Certain of the big tree fig species of western Malesia, mainly stranglers and banyans (*Ficus* sect. *Urostigma*; Figs. 3.3–3.5) are just as attractive and important for birds and mammals. Fifty hornbills of four species have been observed feeding simultaneously in a single fig tree at Gunung Mulu, Sarawak. At Kuala Lompat, Malaya, 60 bird species feed mainly on 38 *Ficus* species in an area of 2 km$^2$. A study[92] at Kutai, east Kalimantan, found that, as at Cocha Cashu, certain figs were the keystone resource for many mammals and birds, and provide the baseline food because they bear fruit throughout the year. Fig fruits are supplemented by fruits of climbers of the Annonaceae and by some Meliaceae and Myristicaceae. At both Kuala Lompat and East Kutai individual fig trees, and indeed species, fruited sporadically, but collectively these figs were always fertile.

It is curious that there is no record of figs as keystone species in the African rain forests. This could be due to a lack of detailed study. If it is a real difference the question then becomes what famine food replaces figs in Africa?

**Carrying capacity and conservation**

Some animal species exist at low population densities either because of the intense competition for food or living space or from the constant attentions of predators. This is true of many inverte-

brates, and also of lower canopy birds, whose total biomass is not dissimilar from that in a temperate forest but is divided between numerous rare species instead of fewer abundant ones. Rain forest birds of the lower canopy characteristically breed seasonally when insect food is particularly abundant, lay only one or two eggs, and have a low rate of success in raising fledglings. Although each species occurs at a low density of only a few pairs per hundred hectares of forest, subadults can be seen wandering around trying to find living space.

Adults are long-lived. It seems likely that a spell of lean years could lead to local extinction of rare species, followed later by re-invasion from adjacent forest when better conditions return. We have little data to substantiate this speculation, and long-term monitoring of populations is required. It is a reason for concern because as rain forests become fragmented into isolated, small, relict patches there may not be enough space for the survival of those species that exist near their lower sustainable limit of density (see p. 188).

## 4.4. Rain forest animals—Chapter summary

1. Rain forests are very rich in animal species. Numbers diminish with elevation and away from the tropics. There are examples between the three regions of convergent evolution, for example amongst specialist frugivorous birds. There are also differences, for example neotropical bat diversity has no parallel elsewhere.

2. American and African rain forests have patches of species richness and of relative poverty. In the Eastern tropics the main zoogeographical pattern is associated with Wallace's Line which separates Asian and Australasian faunas.

3. These many animals coexist in the same forest by sharing the resources in numerous ways. This is shown by considering related groups, for example, primates or bats. Many exhibit preference for a particular layer in the forest canopy, and are active either by day or by night (Fig. 4.4).

There is strong specialization for particular foods. There may be differences in time and place of reproduction.

4. For many rain forest vertebrates fruits are an important food. The amount of fruit varies through the year and the number of animals the forest can support is determined by the amount produced during the lean period. A few so-called keystone species fruit all the year round and provide the baseline food. In American and Asia certain figs are important keystone species.

5. Many animals occur at very low population density and probably suffer local extinction during exceptionally lean periods, but re-invade when conditions improve. Such species are likely to disappear if rain forests are reduced by man to small relict patches.

# 5

Interconnections between plants and animals—the web of life

Animals are dependent on plants for food, consumers on producers, heterotrophs on autotrophs, and forests also provide diverse living space for their animal denizens, as was outlined in Chapter 4. But tropical rain forests are more than just a restaurant and a home. In this chapter we explore aspects of the complex web of interconnections within rain forests which scientists have begun to disentangle over recent years. Plants make use of animals as pollinators (very few are wind-pollinated in contrast to temperate forests), and many use them also as dispersers (though wind dispersal also does occur). It has recently been fashionable to invoke the term co-evolution, in a one-to-one relationship of specialization, as a driving force for species evolution. Some symbiotic relationships do bear this stamp, but in most cases the forces of natural selection are now realized to be more diffuse.

## 5.1. Animals as pollinators[93]

The same combinations of flower and inflorescence features which attract particular pollinators, so-called character 'syndromes', occur in all parts of the tropics. The plant attracts its animal visitors with both nectar[94] and pollen.

Bird flowers are robust and harsh in colour—reds, oranges, yellows, and greens; the nectar is watery and copious. *Heliconia* (Fig. 5.1) is a good example. This syndrome, as others, is recognized by the local birds when a plant is cultivated outside its place of origin. Bird flowers are held away from the leaves, or are borne when the crown is deciduous.

Bat pollination involves two different syndromes. Bat flowers open at night, have viscid nectar, often a musty or sour scent, and are often dull cream in colour. They are either deeply cup-shaped, as in *Durio* and its relative *Kostermansia* (Fig. 5.2) and pollen is conveyed on the bat's head, or else they have a mass of exposed stamens, like a shaving brush, which deposits pollen on to the bat's breast; examples are *Parkia* and *Pseudobombax* (Fig. 5.3). Bats, like birds, cannot easily penetrate foliage and bat flowers are either borne outside the crown, sometimes on long processes—so-called penduliflory shown well by bananas (*Musa*), *Oroxylum*, and *Parkia* (fig. 5.4), or are borne behind the leafy twigs on the limbs (ramiflory; e.g. *Kostermansia*, Fig. 5.2) or on the trunk (cauliflory, Fig. 1.2).

There is sometimes overlap between bat and bird pollination. *Mucuna*, *Spathodea*, and perhaps *Erythrina* are visited by both groups.

Moth flowers, like bat flowers, are mostly nocturnal. They are commonly pale in colour, sweetly scented, and have a corolla tube which is often very long and down which the moth inserts its proboscis to reach nectar produced at the base. *Randia* and other Rubiaceae are good examples (Fig. 5.5).

Beetle flowers, many of them highly fragrant, are as characteristic of the tropics as bee flowers are of temperate and semi-arid lands. Beetles pollinate by clumsy scrambling, eating pollen as they go, and many beetle flowers are open dishes or bowls usually set amongst the leaves. Annon-

aceae, Magnoliaceae, Myristicaceae, and the palm family provide many examples.

Bee flowers, so common in temperate climates, are also extremely common in the humid tropics and are perhaps the major flower-type. Bee flowers are diurnal, often zygomorphic, brightly coloured, sometimes with lines of colour (which may only be visible in ultra-violet light to which bees are sensitive), and are provided with footholds. Orchids, and Leguminosae subfamily Papilionatae are prime examples. Some orchids have evolved exceedingly complex mechanisms, which in some species the intended pollinator has learned to bypass by chewing through the corolla base to reach the nectar.

Foul smelling, mottled, brown and carrion-coloured flowers attract beetles and flies by deception and often trap them; *Amorphophallus* and *Dracontium* (Fig. 5.6), *Aristolochia* and *Rafflesia* (Fig. 3.12) are examples.

A recent discovery is of sequential flowering in species which share the same pollinators. The likelihood of successful cross-pollination is en-



**Fig. 5.1.** *Heliconia indica* in fruit. Solomon Islands.

The robust inflorescence and bracts and the harshly coloured yellow and orange flowers are typical of species adapted to bird-pollination. This is an amphiPacific genus, wild in both Melanesia and the American tropics.



**Fig. 5.3.** *Pseudobombax elliptica* exemplifies the other kind of bat-pollinated flower (cf. Fig. 5.2). Southwest Yunnan, China.



**Fig. 5.2.** *Kostermansia malayana* flowers are nocturnal and ramiflorous. They are pollinated by bats which brush pollen on to their body while seeking at the petal bases for nectar. See also Fig. 5.3. Malaya.

**Fig. 5.4.** *Parkia speciosa* showing the pendulous inflorescences which hang free, where the pollinators can easily reach them without collision with the crown. Planted for its garlic-like seeds. Malaya.

All species of this pantropical genus (Leguminosae, subfamily Mimosoideae) have drumstick-like inflorescences held free of the foliage. This species is bat-pollinated. In others pollination has been recorded by bees, butterflies, birds, or in Africa by the potto, a nocturnal primate.

**Fig. 5.5.** *Ixora lobbii* showing the long corolla tube characteristic of moth-pollinated flowers. Malaya.
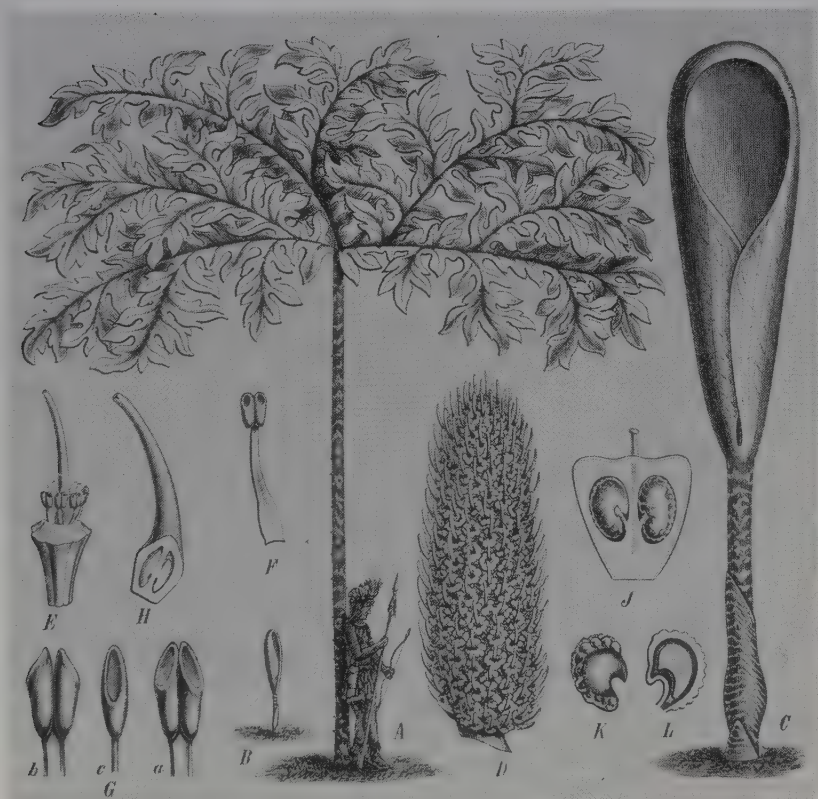


**Fig. 5.6.** The giant South American aroid *Dracontium gigas* with a single multipalmate leaf (A) 4 m tall, and inflorescence (C) 2 m tall. (A. Engler and K. Prantl, *Pflanzenfamilien* II (3) 1889.)

The Old World counterpart is *Amorphophallus* some of whose species are also gigantic.

hanced, firstly by conspecific plants all blooming simultaneously, and additionally, by blooming at a different time from other species. Four of the five *Heliconia* species at La Selva, Costa Rica, share their humming bird pollinators in this manner and with other food-plants (Fig. 5.7). Six closely related *Shorea* in Malaya similarly share the same thrip pollinators[95] and at Pasoh, Malaya, unrelated species pollinated by the same Euglossine (carpenter) bees (*Xylocopa*) have also been discovered to have staggered flowering times (Fig. 5.8).

Deeper intricacies, to promote cross- rather than self-pollination, continue to be discovered. For example, *Oroxylum* in Malaya produces *c.* 18 ml nectar per night but in bursts of 0.05 ml each.[96] This stimulates its bat pollinator to travel from plant to plant, periodically returning, a mode of foraging that has been evocatively termed 'trap-lining' by analogy to a hunter who sets and monitors a line of snares.

A distinction has been discovered between the three nectarivorous bats of Malaya which matches them to the phenology of the species they depend on.[97] Two bats feed on the nectar of plants that flower continually, banana and *Sonneratia* (a mangrove genus). These bats, *Macroglossus sobrinus* and *M. minimus*, respectively, roost singly or in small groups. The third bat, *Eonycteris spelaea* feeds on tree species that only flower once or twice a year, including the important fruit trees durian and petai (*Durio, Parkia*). *Eonycteris* inhabits

caves and lives in huge colonies, which emerge at dusk, like a plume of smoke, from crevices in the rock, and may have to travel many kilometres to feed. Their gregarious living is believed to enable them to communicate to one another the location of patchy food sources. Destruction of forest within the bats' range reduces the food supply, made up of many species each essential for part of the year.
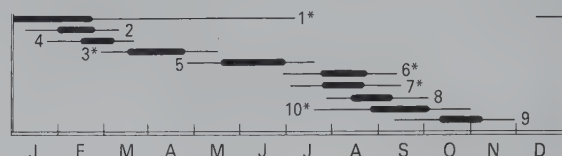


**Fig. 5.7.** Sequential flowering of the undergrowth species fed on and pollinated by helmeted hummingbirds. Lowland rain forest, La Selva, Costa Rica. The five *Heliconia* are starred. (From Stiles 1977.)

1, *Heliconia pogonatha*; 2, *Passiflora vitifolia*; 3, *H. wagneriana*; 4, *Jacobinia aurea*; 5, *Costus ruber*; 6, *Heliconia* sp. 18; 7, *Heliconia* sp. 16; 8, *Aphelandra sinclairiana*; 9, *Costus malortieanus*; 10, *Heliconia* sp. 3.
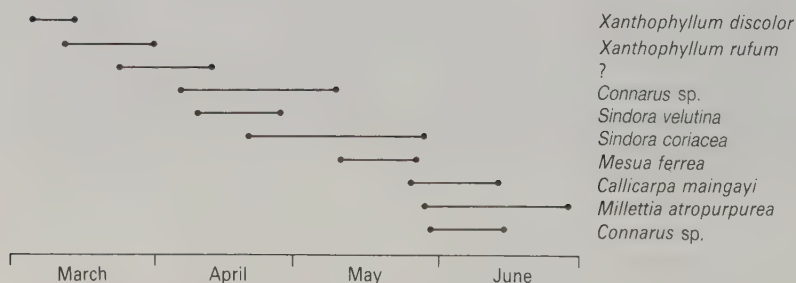


**Fig. 5.8.** Sequential flowering of ten species all pollinated by the same carpenter bees (*Xylocopa*). Malaya. (Appanah 1985.)

## 5.2. Animals as dispersers[98]

Two kinds of bird fruits can be recognized.[99] Non-specialist frugivores feed on fruits with watery, sugary flesh and small seeds, which provide only part of their diet, mostly carbohydrates. These fruits are common in secondary forest, for example Melastomataceae and *Trema*, and the birds that feed on them often congregate in flocks. By contrast fruits evolved for dispersal by specialist frugivorous birds provide a higher quality diet, rich in fats and proteins; the seed is large; many are drupes. Lauraceae contain many examples in all three rain forest regions, plus many palms and Burseraceae in Asia and America. Other specialist bird fruits are brightly coloured, dehiscent, and arillate. This syndrome is found in many families. It is well exemplified by the nutmeg family, Myristicaceae, in which a yellowish pericarp splits open to expose a vivid red edible aril, partly concealing a big black seed (Fig. 5.9). Both types of bird fruit occur in Eleocarpaceae: *Elaeocarpus* has an oily drupe, *Sloanea* fruits are dehiscent and arillate.

There are no well-defined character syndromes for mammal-dispersed fruits (Fig. 5.10). Civets, mongooses, and bears are probably attracted by a strong smell. Colours are often dull and muted. Durian (*Durio zibethinus*), most famous fruit of the East, certainly has a distinctive pungent aroma. Tigers are notorious for their passion for durians. All these animals are mainly nocturnal. The close study of five primate species at Cocha Cashu, Peru (section 4.3), found that, although all fed on fruits, the only common feature the fruits possessed was yellow to orange colour.[100]

It has recently come to be realized that fish are major dispersers of fruits of the riverine forests of Amazonia.[101] They feed during the high water season in the riparian, periodic swamp forests. During the low water season they retreat to lagoons and live largely on accumulated fat. No particular features characterize fish-dispersed fruits. Two species of rubber tree, *Hevea brasiliensis* and *H. spruceana*, have seeds that are a major food source for certain Amazonian fish. They occur in seasonal swamp forest (and in the case of *H. brasiliensis* also on dry land), and have big fruit capsules that



**Fig. 5.9.** *Myristica fragrans*, the nutmeg, has fruits adapted for dispersal by specialist frugivorous birds (Blume 1835, plate 55.)

The fawn fruits dehisce to expose a single, big black seed, partially enclosed in a finely divided, scarlet aril.

dehisce explosively to disperse the 20- to 40-mm-diameter seeds for 10 m or more. Some seeds fall on dry land. Fish congregate below the trees to catch the rest. Seeds that escape predation float until the floodwaters recede, at which time they reach the soil surface and germinate.

The relationship of particular animal dispersers to particular fruit-bearing plant species is less close than with pollination. Temporal partitioning has however been discovered. For example, in Trinidad there occur 19 bushy epiphytic *Miconia*

**Fig. 5.10**. The siamang (*Hylobates syndactylus*), a large ape of Malaya and Sumatra (weight 9–12 kg), seen here feeding on *Aglaia*, includes much fruit in its diet.

species, Melastomataceae, which bear brightly coloured sugary fruits, typical of the family. Each species only bears fruit for a short period and these periods do not overlap, which enhances the likelihood of dispersal for any particular species.[102] It is, however, difficult to determine how much

selection pressure there has been to evolve non-overlapping fruiting periods because, with nineteen species each of which only fruits for a short while, there is a strong probability periods will not overlap purely by chance.

## 5.3. Plant webs, mobile links, and keystone species

A rain forest may be universally green and monotonous to our eyes but a herbivore sees it as a poisonous place with patches of alkaloid, saponin, or siliceous spicules, and seeks out what it can safely eat.[103] Plants have evolved toxins that deter herbivores, and related groups are constrained by their genetic constitution to manufacture similar chemicals. Thus, for example, Apocynaceae are rich in alkaloids,[104] especially in the milky latex that nearly all possess. Drug companies exploit these similarities when screening forest plants for potential new medicines. Instead of an expensive blind search they concentrate on those families most likely to be of interest.

Herbivores have evolved adaptations to be able to detoxify particular chemicals. Thus there have arisen guilds of insects all specialized to feed on a particular group of related, and therefore chemically similar, plants. Such a group may be called a plant web.[105] In the forest many parallel insect guilds coexist on these different plant webs, without overlap of feeding sites.[106] In some cases the insects utilize the chemicals they ingest. Birdwing butterflies and some other Papilionidae feed on the herbaceous climbers of family Aristolochiaceae which provide them with a distasteful chemical and render them unpalatable to predators. The butterflies can therefore afford to congregate near the plant, and this facilitates mating. They are mimicked by other butterflies and also by day-flying moths.

Two complex plant webs have been disentangled in the neotropical rain forests, one involving Solanaceae and the other Passifloraceae.[107]

There are *c.* 500 species of Passifloraceae in the New World tropics, as wiry climbers and small trees; *Passiflora* is the biggest genus. The main insect feeders are Heliconiine butterflies, along

with flea beetles, coreid bugs, and diopterid moths as less important herbivores. At any one locality there are between ten and fifteen passiflores of various habits and occupying different habitats. These are pollinated and dispersed by generalist bees, birds, bats, and moths. The pollinators and dispersers cannot obtain their food solely from Passifloraceae because flowering is sporadic. Instead they feed on species of different plant webs at different times of year, and thus may be called mobile links because they bridge otherwise unconnected components of the forest ecosystem.

If a forest is degraded partly to pasture, which is happening extensively in parts of the neotropics (Chapter 10), some of the local passiflore species disappear along with their habitat. Likewise, if an area becomes entirely climax forest, there is also a loss of diversity in the plant webs and a parallel loss in the dependent insect guild. Moreover, Heliconiine butterflies are the principal model for major mimicry complexes so loss of any of these butterflies diminishes the numbers of the (edible) mimics.

The plant web and associated insect guild on neotropical Solanaceae is similar. In this case Ithomiine butterflies are the principal feeders and mimetic model.

Another dimension of complexity is that the mobile link species which are essential to the reproductive success of the plants of several separate plant webs, are themselves commonly totally dependent on a few keystone species for providing their food at times when nothing else is available. The importance of some figs as keystone species for birds and mammals was described in section 4.3. The continuously flowering pioneer forest-fringe shrub *Melastoma malabathricum* is today a

keystone species at Pasoh, Malaya, for Euglossine bees which are heavily dependent on it during lean periods. When the primary forest burst into heavy flower in late 1981 these bees were observed to migrate from the secondary scrub with which the remaining primary forest is now surrounded on to the new ephemeral rain forest food source.[108]

In America Euglossine bees are important mobile links. Thirty to fifty species may occur together and any one bee species may pollinate a dozen plant species, including orchids and aroids. Trap-lining (p. 70) is common. Orchids provide pheromones to male Euglossines which are essential for courtship and hence mating. The loss or absence of orchids thus causes the ecosystem to start to unravel. The failures to set fruit of plantation-grown Brazil nut trees is a good example of these intricate interactions.[109]

The Brazil nut (*Bertholletia excelsa*) is pollinated by Euglossines. However, these bees need some other source of pollen for the 11 months when it is not in bloom, and they also need epiphytic orchids to complete their own life cycle. Wild Brazil nut trees occur scattered through the forest. When concentrated in isolated mono-specific plantations or remaining as relict trees after forest destruction they do not have the linkages essential for their success. The huge, thickly woody fruits weigh several kilograms and fall heavily to the ground. They contain 10–20 strongly armoured seeds, the Brazil nuts of commerce. The final link in the Brazil nut life cycle is the agouti (*Dasyprocta*), a giant rodent, which gnaws open the outer carapace and stores the nuts in caches scattered through the forest. Agoutis forget some of their nut hoards, which is how the scattered distribution of Brazil nut trees arises.

If any one plant-web becomes particularly abundant, insects of its feeding guild will find it easy to locate in the forest and may increase in numbers. 'Pest pressure' is likely always to keep any particular plant-web at a low density, below a threshold at which it becomes too 'apparent' to its herbivores. This is one mechanism that maintains high species diversity in many ecosystems, including tropical rain forests. One particular case of the reduction of tree seedling population density is discussed later in section 7.3.

## 5.4. Co-evolution

Extreme richness in species of plants and animals is one of the best known features of tropical rain forests. How it has arisen is one of the questions that scientists find perpetually fascinating about these ecosystems. It is a question that has therefore sparked off a plethora of discussion and speculation.

Co-evolution, i.e. close relationships between invidual plant and animal species, has been invoked as a major motor of species evolution.[110] An arms race has been postulated in which an insect species succeeds in detoxifying a protective chemical, feeds well, and multiplies until the plant responds to this pest pressure by evolving a new toxin. This is chemical warfare and its extreme form has sometimes been called the Red Queen Hypothesis—because 'it takes all the running you can do to stay in the same place'.[111] But such stepwise co-evolution seems, on inspection and reflection, to be improbable. In fact, pest pressure from the plant's point of view is general, and toxic chemicals are developed against all its herbivores. 'Arms races' are unlikely to proceed as relentless and progressive bouts of defence and counter-defence. They are likely to be much more erratic and to lead to the development of groups of mutually dependent plants and animals, the plant-webs and their associated herbivore guilds which were discussed above.

Speculation that particular ecological species groups of trees are more likely to have their leaves chemically defended against herbivores than others has also not survived scrutiny. Chemicals that are possibly toxic are indeed commonly present, but it now seems likely that mechanical toughness rather than chemical composition is the most important deterrent to insect herbivory. Most loss of leaf area in fact occurs before full

expansion of the lamina has taken place, because young leaves, which are soft and not fully formed, are especially susceptible.

A study at Barro Colorado Island, Panama, demonstrates these general conclusions.[112] There, 70 per cent of the 46 species investigated had young leaves damaged more than mature ones. Even though their content of phenolic compounds was 2.3 times higher, they were less tough and fibrous. In the same study mature leaves of the pioneer species were grazed six times more rapidly than those of climax species, and were also found to be less tough and fibrous.

## Symbiosis

There are various different rain forest examples of symbiotic associations between ants and plants. These are clear instances of co-evolution in the two partners. Several Old World epiphytes of family Rubiaceae (*Hydnophytum*, *Myrmecodia*, and relatives; Fig. 5.11) have swollen tubers, like



**Fig. 5.11**. The ant-plant *Myrmecodia tuberosa* with its swollen stem cut open to show the internal chambers in which the ant *Iridomyrmex cordatus* lives. Note covered ant-runs on tree trunk. New Ireland.

irregular knobbly hand grenades, with chambered, hollow interiors that are ant-inhabited. The excretions of the ants and the humus that they accumulate nourish the plant.[113] Other epiphytes may grow on the humus. In the New World tropics certain tree-living ant species collect seeds of various epiphytes and plant them on their earthen nests to form aerial 'ant gardens'.[114] They collect animal faeces to nourish the plants which reward them by production of starch grains or sugary secretions from extrafloral nectaries. Ant gardens are particularly abundant in heath forest.

Certain climbing rattan palms are associated with ants. Some *Korthalsia* species have a swollen modified woody ligule, or ochrea, within whose concave interior the ants dwell. Should one accidentally brush against an ant-*Korthalsia* it emits a curious whispering, rustling, rattling noise, as the ants all rush out and beat their mandibles on the hollow box against the attack. In other rattans, species of *Calamus* and *Daemonorops*, ants make nests amongst the bases of interlocking plates of spines on the leaf sheaths (Fig. 5.12), but no benefit to the palm has been demonstrated.

The West African rain forest treelet *Barteria fistulosa* is defended against large browsing herbivores by the ant *Pachysima aethiops* whose sting can penetrate elephant hide and which numbs lesser mammals, including man, for several days.

The genera of pioneer trees *Cecropia* (New World; Fig. 7.5) and *Macaranga* (Old World, mainly Malesia; Figs. 7.6, 7.7) both have numerous species that harbour ants. In the case of several *Macaranga* species a single species of ant, *Crematogaster borneensis* var. *macarangae*, inhabits the hollow apical internodes (Fig. 5.13), where it keeps scale insects (mainly *Coccus penangensis*) which tap the tree's sap. The trees produce starch grains on the edges of their recurved stipules on which the ants feed. Experimental removal of ants has led to these *Macaranga* spp. being attacked by leaf-eating insects. Furthermore, these ant macarangas are usually free of epiphytes and climbers because the ants bite off any part of a foreign plant that comes into contact with their host (33 per cent of uninhabited *Macaranga triloba* in Malaya had climbers on them compared to only 5 per cent of ant-inhabited ones).[115] The ant-*Macaranga*
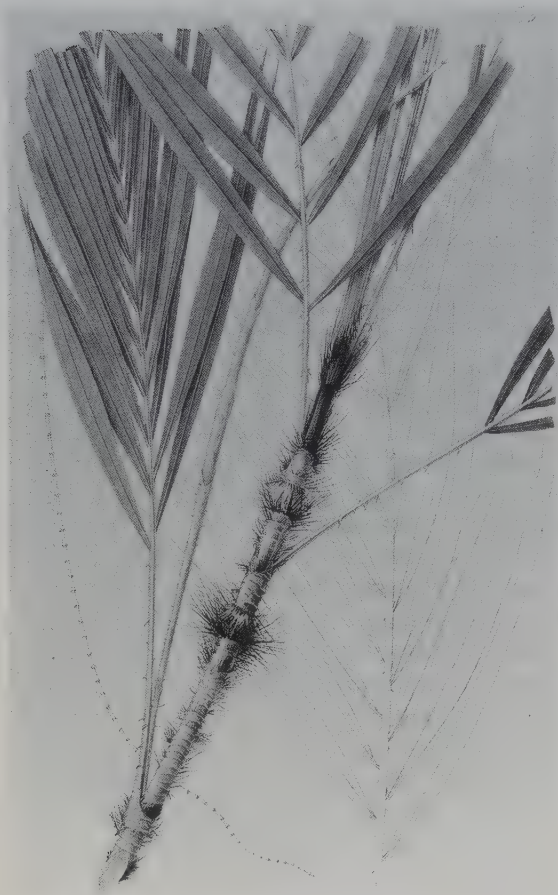
**Fig. 5.12.** The climbing rattan palm *Daemonorops crinita* of Borneo and Sumatra, showing the interlocking combs of spines in whose bases ants make their nests. (Blume 1835, plate 136.)
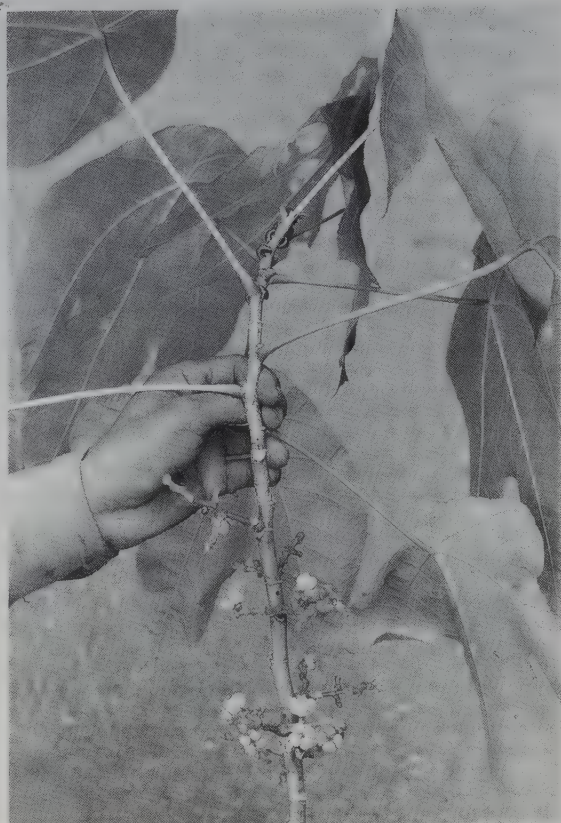


**Fig. 5.13.** *Macaranga triloba* showing the holes made in the internodes by cohabiting ants. Note also the recurved stipules on whose margins starch grains form which the ants feed on. West Malesia.

story has a further twist. Plants of several *Macaranga* species have been found with their leaves badly eaten despite the presence of ants. Very careful searching has shown that the culprits are tiny caterpillars of the Lycaenid butterfly *Arhopala*, with never more than a few on any one tree. The caterpillars produce a sugary secretion when touched by an ant, so are tolerated. They are coloured like the stipules or leaf nerves of the *Macaranga* and in this way escape predation. The butterfly has evolved to parasitize the ant-*Macaranga* symbiosis.[116]

Other equally complex mutualisms have also been discovered that do not involve ants. One such is between Passifloraceae and Heliconiine butterflies.[117] The butterfly lays its eggs on young shoot tips and the caterpillars feed there. The mother butterfly seeks out unoccupied plants but the plants have evolved either yellow extrafloral nectaries that mimic eggs, or orange-yellow modified stipules that imitate young caterpillars. Heliconiine butterflies have evolved an acute sense of vision and an ability to learn. It can be observed that they counter these defences by probing potential laying sites with their antennae and forelegs to see if they are really occupied. The Passifloraceae have exceptionally polymorphic leaves, variable both within and between species; it is claimed this enables them to escape detection by the butterflies. What lends credence to the claim

**Fig. 5.14.** The pollination of fig flowers is one of the most intimate plant-animal relationships known. (Partly after Corner 1988, Figs. 162, 164.)

Special fig wasps, a different species for every species of fig, develop inside gall flowers *(A)*; and bite their way out *(B)*; they mate inside the fig *(C)*; the male dies but the female crawls out of the mouth of the fig, getting pollen on her body as she passes the male flowers *(D)*; she flies to another tree, probably attracted by the scent of young figs *(E)*; the young fig either contains female flowers with long styles and these are pollinated *(F)* so develop a seed *(G)*, or the fig may contain sterile gall flowers with short styles down which the female inserts her ovipositor and lays an egg *(H)*; this hatches, the grub feeds on the gall flower ovary and develops into either a male or female wasp, which then repeats the cycle.

for parallel evolution with considerable mutual influence between butterflies and passiflores, is that the more complex avoidance and detection systems occur in both the insect and the plant in those species which taxonomy suggests are more highly evolved, whereas the most primitive species have the simplest adaptations.

A particularly close symbiosis is that between figs and the wasps that pollinate them. Every species of fig has its own wasp, and where a fig tree is cultivated outside the range of its pollinator fertile seeds fail to develop. This intricate microcosm of evolution is described in Fig. 5.14. As a further complication some wasps have a species-specific parasite (Fig. 5.15).

## 5.5. Implications for forest conservation

Tropical rain forests are becoming fragmented into small relict patches or simplified in structure and composition by exploitation for timber, as will be discussed further in Chapter 10. Interconnections between plants and animals in the ecosystem, which are only now beginning to be studied, are essential for its functioning, and are prone to disruption. The ecosystem may then slowly collapse. Trees live for perhaps a century or more (Fig. 7.30), so are likely to persist for decades after potential pollinators and dispersers have gone. At the Sungei Menyala forest in Malaya, which consists of only a few relict hectares as an island in a sea of rubber plantation, fleshy mammal-dispersed fruits of *Chrysophyllum lanceolatum* nowadays lie in piles around the parent tree.[118] That forest, which to the casual observer still looks fine, is in fact breaking down. However, as was discussed above, plant species are not always dependent on only a single animal species for pollination or dispersal; where relict forest patches occur which are big enough to retain some suitable animals and where hunting has not exterminated them, the ecosystem may continue to function even though it has an incomplete species assemblage.

## 5.6. Plant breeding systems

Plants have evolved the various syndromes of flower and inflorescence characters described above, to attract particular animal pollinators which then convey pollen from flower to flower. Where pollination occurs between different plants the amount of genetic recombination is high. These are so-called out-breeding species. Genetic recombination is less in self-pollinated species, so-called inbreeders, in which flowers on the same plant are involved, and is zero in apomicts, viz. those species whose reproduction bypasses the sexual process (although many apomictic species do also reproduce sexually on rare occasions).

The question has been debated whether the prevalence of one particular breeding system is the driving force that accounts for the enormous richness in plant species of tropical rain forests. A. Fedorov observed that many rain forest species occur as scattered individuals, and speculated that cross-pollination is low or negligible with the result that inbreeding or apomixis prevails. As mutations occur over the course of time the isolated populations evolve into different species. P. S. Ashton countered Fedorov with the opposite view. He believed cross-pollination prevails to give high gene flow between individuals. Each generation is genetically diverse as a result of out-breeding and is operated on by selection, with resulting strong specialization for different niches in the forest ecosystem.[119]

There are in tropical rain forests some genera with many sympatric species and these could have arisen from either mechanism. One of the best known species-rich families is Dipterocarpaceae, and in any one west Malesian lowland rain forest up to twenty or so species mainly of *Dipterocarpus*, *Hopea*, and *Shorea* commonly coexist. Other Malesian examples are *Polyalthia* (Annonaceae), *Calophyllum* and *Garcinia* (Guttiferae), and *Syzygium* (Myrtaceae). Further instances are *Eschweilera*, *Inga*, and the forest floor palms *Geonoma* of the neotropics, and in West Africa *Diospyros* and *Drypetes*.



**Fig. 5.15.** The fig to wasp relationship is rendered even more complex by parasitic insects called Inquilines which lay their eggs inside the developing fig wasp grub by pushing their very long ovipositor through the wall of half-grown fig fruits right into a gall flower. (Corner 1988, Fig. 164.)

**Fig. 5.16.** *Garcinia mangostana* (mangosteen) of Malesia has extremely uniform fruits; the species reproduces apomictically. Malayan wayside fruit stall.

Various studies on breeding systems in rain forest trees now cast light on the questions raised by Fedorov and Ashton. An investigation of dipterocarp breeding systems in Malaya[120] demonstrated two apomictic species, five probable apomicts, sixteen with slight or only tentative evidence, and seven with negative evidence for apomixis. In addition ten species were cross-pollinated and a further two probably so. Apomixis is well-known in cultivated rain forest fruit

trees, namly in citrus, clove (*Syzygium aromaticum*), mangosteen (*Garcinia mangostana*; Fig. 5.16), duku, langsat (*Lansium domesticum*), and mango (*Mangifera*), and probably occurs in wild *Garcinia* and *Syzygium*, both of which genera have numerous sympatric forest species.

By contrast dioecism, the occurrence of male and female flowers on different plants, ensures that cross-pollination must occur. It is found in many rain forest species, e.g. many Ebenaceae, Euphorbiaceae, and Myristicaceae. Meliaceae and Sapindaceae whose flowers look hermaphrodite are in fact functionally dioecious. At La Selva, Costa Rica, 23 per cent of 333 tree species were dioecious, and 26 per cent of the 711 tree species with stems 0.1 m in diameter or over were dioecious on an 8.8 ha study area in Sarawak.[121]

Apomicts are obligate inbreeders. Dioecious species are obligate outbreeders. However, in a species that is outbreeding most gene flow is in fact restricted to short distances. This has been demonstrated in rain forest in a study of isoenzymes and of morphological variation in the leaves of the small tree *Xerospermum intermedium*, and isoenzymes of the emergent tree *Shorea leprosula* at Pasoh, Malaya; it was found that the further trees are apart the more they differ.[122] It appears that most pollination occurs between near neighbours and most seeds fall near the parent tree.

The conclusion from all these studies is that rain forests, like other ecosystems, have a diversity of breeding systems and therefore no single one is the driving force of species evolution. All kinds of breeding systems contribute to species richness, none offers an exclusive mechanism. The patterns of genetic variation in the forest confirm, however, that there is restricted gene flow in the few species studied.

## 5.7. Interconnections between plants and animals—Chapter summary

1. Numerous animals coexist in tropical rain forests by subdividing its food resources. There has been loose co-evolution between plants and animals.

2. Flowers have developed the same syndromes of features for particular groups of pollinators in all parts of the tropics, and we can distinguish bat, bird, beetle flowers, etc.

3. There are also syndromes of fruit characters, likewise pantropical, each adaptive to particular dispersers.

4. Some plant species that have the same pollinators or dispersers coexist by flowering or fruiting at different times.

5. Related plants have similar defensive chemicals and form plant webs, each one fed on by a particular guild of insects evolved to detoxify those particular compounds. 'Pest pressure' is likely to prevent members of any one plant web becoming particularly abundant. Several plant webs may share the same pollinators or dispersers, which have been called 'mobile links'. At lean seasons these depend for food on plants that are fertile when little else is, the so-called 'keystone species'. Both mobile links and keystone species are essential for the maintenance of full ecosystem diversity.

6. Closer co-evolution is less common. Ants and rain forest plants have evolved several kinds of mutualism. New World Heliconiine butterflies and Passifloraceae have co-evolved and the simpler adaptations in both partners are in the more primitive species. Figs and their pollinating wasps show one-to-one species relationships (Fig. 5.14).

7. All kinds of plant breeding systems found in other biomes exist side by side in tropical rain forests. No single breeding system can be invoked as the mechanism that has generated high species richness.

8. Where man reduces rain forests to small fragments or over-exploits them there is a loss of complexity and diversity, the web of interconnections unravels. For example, Amazonian fish need swamp forest fruits; durians are pollinated by bats that need other pollen sources for the 11 months when durians are not in flower; guilds of Heliconiine butterflies and their mimics become impoverished if their food-plant Passifloraceae begin to disappear because of loss of habitat.

# Tropical rain forests through time

The great contrast between the two divisions of the archipelago is nowhere so abruptly exhibited as on passage from the island of Bali to that of Lombock, where the two regions are in closest proximity. In Bali we have barbets, fruit-thrushes, and woodpeckers; on passing over to Lombock these are seen no more, but we have an abundance of cockatoos, honey-suckers, and brush-turkeys which are equally unknown in Bali or any island further west. The strait is here fifteen miles wide, so that we may pass in two hours from one great division of the earth to another, differing as essentially in their animal life as Europe does from America.

A. R. Wallace *The Malay archipelago*, (3rd edn.), 1872.

Patterns of distribution of plants, animals, and vegetation have long fascinated biologists. Their detection is part of the search for generalizations about Nature, the reduction to simplicity of initially bemusing variety. The scientist then goes on to seek for the causes of the patterns he has detected. Over the past few decades two major causes have been discovered for many of the present-day patterns seen amongst rain forest plants and animals. These are continental drift, and past fluctuations of climate; both have contributed to a recent revolution in our understanding of tropical rain forest biogeography.

## 6.1. Palaeogeography

The occurrence of separate continental plates that have drifted by ocean-floor spreading is an established fact.[123] Plate tectonics causes the super-continent Pangaea to break up from about 180 million years ago (mid-Jurassic) onwards (Table 6.1, Fig. 6.1). The northern and southern halves, Laurasia and Gondwanaland, continued to fragment and today's arrangement of land and sea was not achieved until about late Tertiary, approx. 10 million years ago.[124] The break-up of Gondwanaland is of special significance for the tropical biogeographer because all three tropical regions lie on its fragments. Thus, continental drift has had powerful influences on patterns of distribution of families, genera, and species.

**Gondwanan ranges**

Similarities in flora between the three regions of tropical rain forest, described in general terms in Chapter 2, occur because all are part of old Gondwanaland. The major evolution of the flowering plants had occurred before Gondwanaland began to break up and has continued on the different fragments. Today 334 genera and 59 families of flowering plants are essentially pantropical. Looking more closely other patterns can be seen too.

*Campnosperma*, has a typical Gondwanan distribution. This genus of light-demanding lowland rain forest trees occurs in Panama, Colombia, Brazil, Madagascar, Seychelles, and from India to Micronesia. Absence from continental Africa is believed to reflect massive extinctions there due to periods of strongly dry climate.

Disjunct ranges, with one part of a plant-group occurring on the Guyana Shield of northern South America and the other in Malesia, are also believed to reflect descent from a pan Gondwanan ancestor, with extinction in Africa. Examples are Bonnetiaceae, a family of small trees (*Bonnetia* America, *Ploiarium* Asia), and Tetrameristaceae, with *Pentamerista*, recently discovered in Guyana, as a relative of the well-known peat swamp forest species *Tetramerista* (punah) of western Malesia.

Table 6.1

*Geological periods and epochs mentioned in the text*

| Million years | Period | epoch | |
|---|---|---|---|
| | Q | Pleistocene* | |
| 2.0 | | | –Andes mountains completed |
| 5.1 | | Pliocene | |
| | | Miocene | –collision at/near Sulawesi creates modern Malesia |
| 24.6 | Tertiary | Oligocene | |
| 38 | | Eocene | –Atlantic nearly formed (Fig. 6.1c) |
| 54.9 | | Palaeocene | |
| 65 | | | |
| | | Upper | |
| 97.5 | Cretaceous | | |
| | | Lower | |
| 144 | | | –Gondwanaland and Laurasia starting to break up (Fig. 6.1b) |
| | | Late | |
| 163 | Jurassic | | |
| 180 | | Mid | –Pangaea starts to break up (Fig. 6.1a) |

Q=Quaternary      * Last 10⁴ years of Quaternary is the Holocene

The geographical distribution of Dipterocarp-aceae also reflects a Gondwanan ancestory. Subfamily Dipterocarpoideae contains the important big timber trees, pre-eminent in today's international timber trade and on which so much of the discussion in this book is focused. They range from Malesia westwards to India and Sri Lanka, with one outlying endemic genus in the Seychelles and fossils in Somalia and Uganda. Subfamily Monotoideae are small trees of subSaharan Africa, mainly of seasonal forests.[125]

There are other groups besides Dipterocarp-aceae which span the southern Indian Ocean, occurring on fragments of old Gondwana. The fan palms *Borassus* and its allies are one example (Figs. 6.2, 6.3), *Nepenthes*, the pitcher plants (Fig. 4.7), found in Madagascar and Seychelles as well as Malesia, are another.

Another common pattern is a geographical range that spans the southern Atlantic Ocean, with representatives in both tropical America and

tropical Africa.[126] Twelve families of flowering plants are essentially limited to these two regions, and in many cases are much more numerous in one; for example Bromeliaceae and Cactaceae which are mainly American but have a few Old World species. One hundred and ten genera have the same amphiAtlantic range, e.g. *Annona*, *Chlorophora*, *Ocotea*, and the palms *Elaeis* and *Raphia* (oil palm, raffia).

### Closure of the eastern Tethys Ocean[127]

Gondwanaland and Laurasia were separated by the great Tethys Ocean. Tethys was closed by the northwards movement of parts of Gondwanaland (Fig. 6.1). First Africa and then India drifted north and collided with the southern margin of Laurasia. Further east the continental plate which comprised Antarctica/Australia/southern New Guinea moved northwards, broke in two leaving Antarctica behind, and collided with the southeast extremity of Laurasia, at about 15 million years ago, the mid-Miocene; this created the Malay archipelago (Malesia) as it exists today. Both super-continents had their own set of plants and animals.

India rafted Gondwanan plants northwards and after collision these mixed with Laurasian ones to give the dual-origin flora of that region today. The collision within Malesia was at or near what is the modern island of Sulawesi. Western and eastern Malesia have very different animals, demarcated by a very sharp boundary, Wallace's Line (Figs. 6.4, 6.5). The strength of Wallace's Line as a boundary varies with the ease with which the animal group under consideration disperses over salt water. Present day zoogeography is a clear reflection of the plate tectonic history. Plants do not divide so sharply at Wallace's Line, presumably as a result of their ability to disperse over water, but Laurasian and Gondwanan groups can be recognized (Figs. 6.6, 6.7), centred in western and eastern Malesia, respectively.

Both Laurasian and Gondwanan floristic groups occur in the tropical rain forests of Queensland, northeast Australia. Recent research has shown that Laurasian elements were well represented there before the mid-Miocene collision and there was no sudden influx. It is believed that

**Fig. 6.1.** Continental drift. (a) Mid Jurassic: Laurasia (north) and Gondwanaland (south) in contact as Pangaea, separated in the east by the Tethys Ocean. (b) Lower Cretaceous: Gondwanaland breaking up and Laurasia starting to do so. Tethys Ocean being closed. Australia/New Guinea still joined to Antarctica. (c) Late Eocene: Atlantic Ocean nearly formed; Tethys Ocean much smaller; Africa and India have nearly collided with Laurasia; Australia/New Guinea has separated from Antarctica but the Malay archipelago has not yet formed. (Smith and Briden 1977; present-day coastlines and continental shelves shown, Mercator projection.)
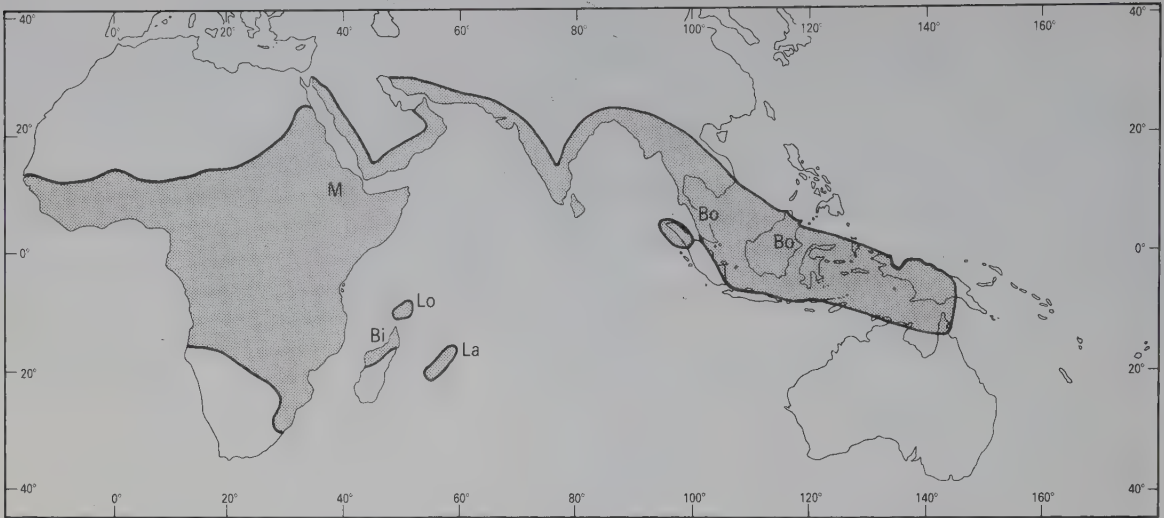
**Fig. 6.2.** The fan palms of tribe Borasseae originated on Gondwanaland. They continued to evolve as it broke up and occur today on its Old World fragments. Outline, *Borassus* and *Hyphaene* (10 spp. each), both widespread and probably with ranges extended by man. *Bi, Bismarkia* (1 sp.); *Bo, Borassodendron* (2 spp.); *La Latania* (3 spp); *Lo Lodoicea* (1 sp., the double coconut). *Medemia* (1 sp. last seen 1964, probably extinct). (After Uhl and Dransfield 1987.)

**Fig. 6.3.** *Borassus flabellifer*, the lontar palm, here seen planted in east Malaya and exhibiting the deep, oblong crown of youth.



**Fig. 6.4.** Wallace's Line, which runs between Borneo and Sulawesi, marks the boundary between the Asian and Australasian faunas of Laurasian and Gondwanan ancestry, respectively. (After Whitmore 1984*a*, Fig. 1.9.)

(a)

(b)

**Fig. 6.5.** Wallace's selection of animals to demonstrate the two distinct faunas that occur in Malesia. These are (left to right and top to bottom) (a) Borneo: the western tarsier *Tarsius bancanus*, one flying lemur *Cynocephalus variegatus* in flight and another one seated, the pentail treeshrew *Ptilocerus lowii*, the malay tapir *Tapirus indicus* and a couple of lesser mousedeer *Tragulus javanicus*; (b) New Guinea: a tree kangaroo *Dendrolagus inustis*, the fairy lory *Charmosyna papou*, the twelve-wired bird of paradise *Seleucides melanoleuca*, the common paradise kingfisher *Tanysiptera galatea*, and a crowned pigeon *Goura cristata* (*coronata*) (Wallace 1876, Vol. 1.)

this was because fragments broke off the continental margin of northern Australia and drifted northwards, from the late Jurassic onwards (Fig. 6.8), and that these provided stepping stones for the movement of plants and animals before the final closure of Tethys.

### The northern Andes

Another result of plant tectonics, which has left its mark on neotropical rain forest biogeography, is the creation of the Andes which continued till the end of the Pliocene, 2 million years ago. The Andes arose by the progressive uplift of the western edge of South America as it overrides the edge of the Pacific continental plate which is being pushed under, a process known as subduction. The consequence has been to divide in two the ranges of lowland rain forest species, so that today they are disjunct with one part in the Pacific coast rain forests and the other part in the Amazonian forests. In many groups there has been evolution since the range became broken so that the two parts are no longer identical. An example, the vegetable ivory palms, subfamily Phytelephantoideae, is shown in Fig. 6.9.
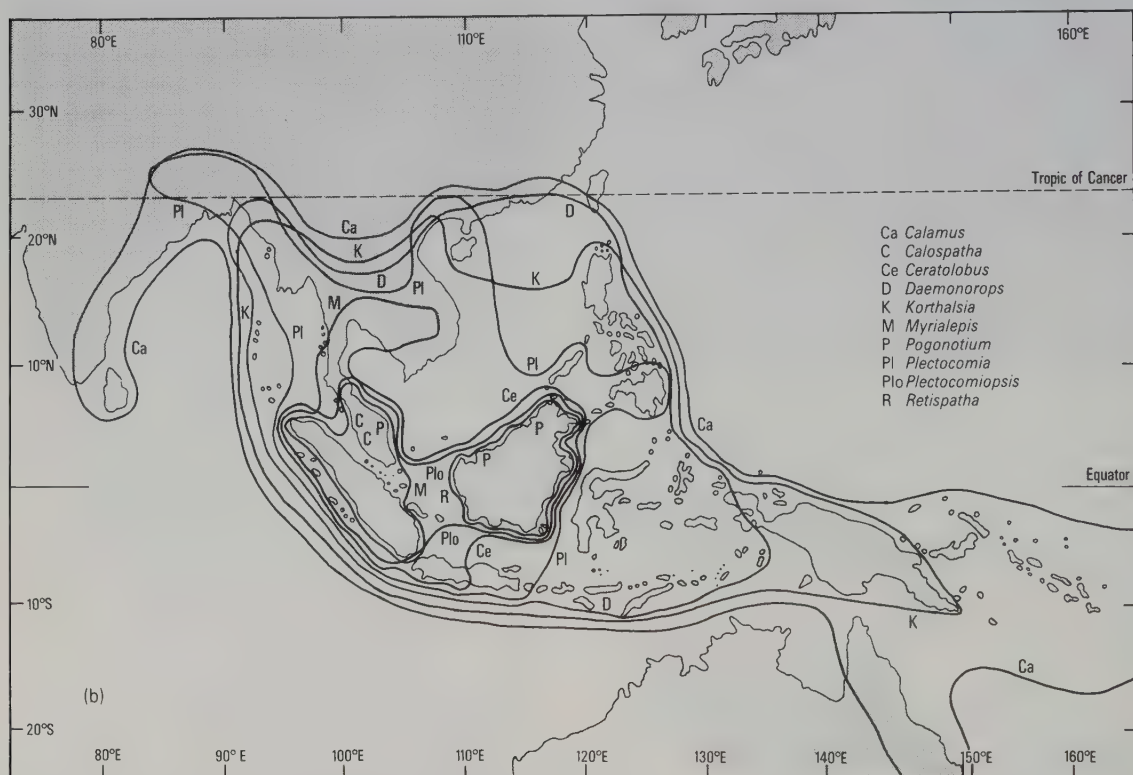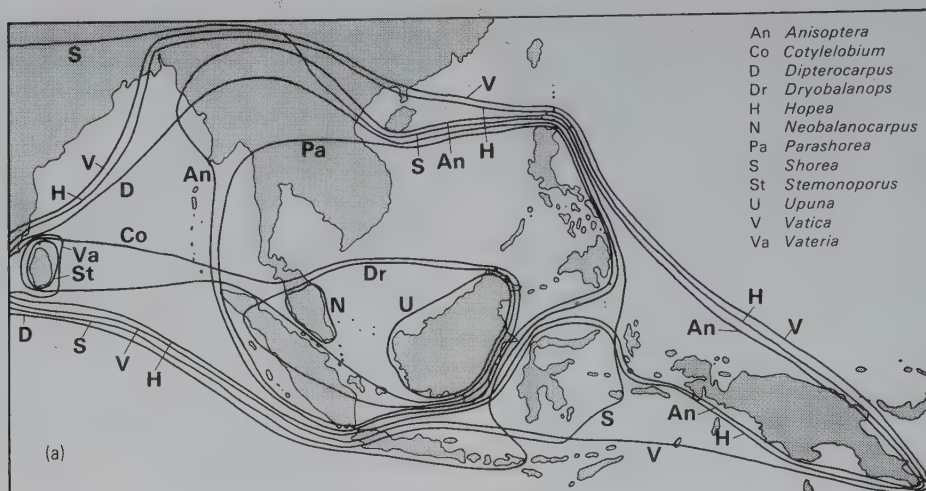
**Fig. 6.6.** Plant geography of Malesia derived from plate tectonics. (a) Dipterocarpaceae and (b) the climbing palms (rattans) are centred on the western, Laurasian, part of Malesia, whereas (c) Winteraceae have an eastern, Gondwanic, centre of distribution. (Whitmore 1981, Figs. 8.3, 6.7, 8.9.)

Be *Belliolum*
B *Bubbia* (also 1 in Madagascar)
D *Drimys* (also 4 in N. America)
De *Degeneria*
E *Exospermum*
P *Pseudowintera*
T *Tetrathalamus*
Z *Zygonium*
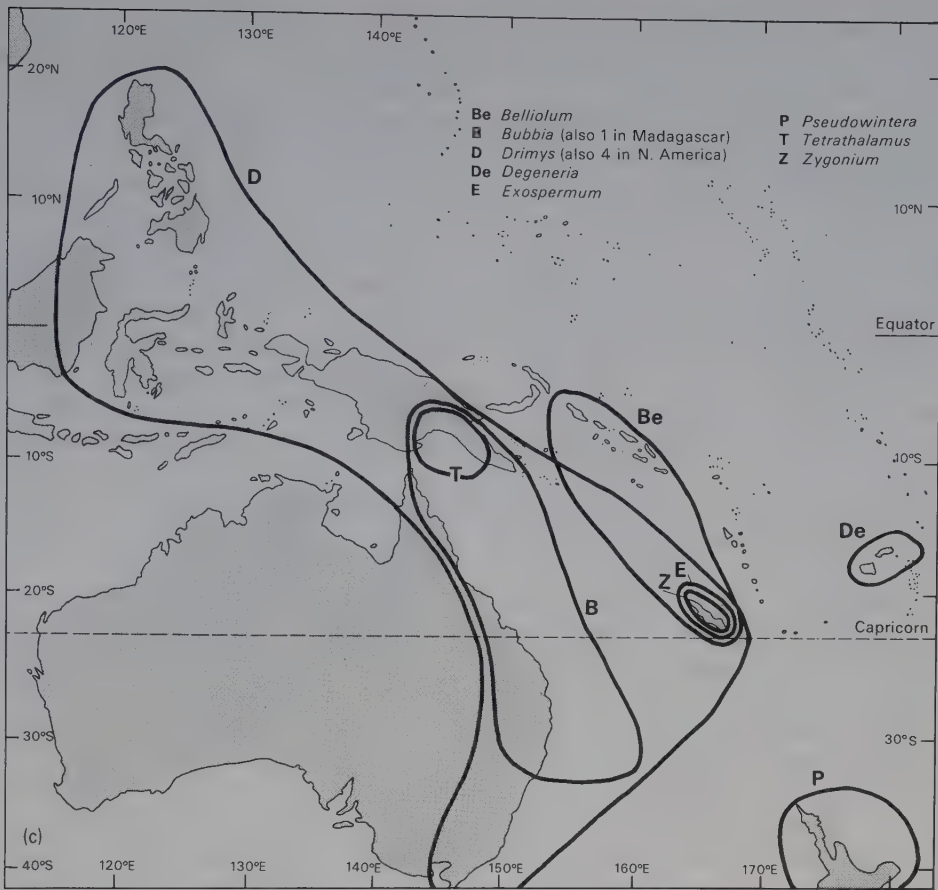
## 6.2. Palaeoclimates

The climate of the tropics has been continually changing. The old idea of fixity is quite wrong; climatic changes have had profound influences on species ranges.

### The Quaternary

Most knowledge about past climates is for the last 2 million years, the Quaternary period, during which there has been repeated alternation at high latitudes near the poles between Ice Ages or Glacial periods and Interglacials. During Glacial periods tropical climates were slightly cooler and drier, with lower and more seasonal rainfall. During these times rain forests became less extensive and seasonal forests expanded. Most of the Quater-

nary was like that; present-day climates are extreme and not typical of the period as a whole. Today we live at the height of an Interglacial, the global climate has got progressively warmer during the last 10 000 years, the period known as the Holocene, and the last Glacial maximum (the Wisconsin-Würm Glaciation) was about 18 000 years ago (before present, BP). At the Glacial maxima sea levels were lower by as much as 180 m because much water was frozen in the greatly extended polar ice caps. In Malesia the Sunda shelf, extending from the Asian continent, and the Sahul shelf, reaching out from New Guinea, were both exposed (Fig. 6.4), so the separate islands west of Wallace's Line became joined as one land mass and those to the east as another. The islands

of the Caribbean also became partially joined. Sea surface temperature was slightly cooler than today, by 2°C at 18 000 BP in the tropics.

The evidence for past differences in climate in the tropics is two-fold, from the record of past vegetation deduced from palynology, and from direct physical traces.

*Palynology.*[128]   There are montane peat deposits in former lakes in all three tropical regions. Pollen from nearby vegetation gets incorporated in peat as it forms and can be extracted for study. The picture revealed by pollen analysis of peat from a site at 2600 m near Bogota, Colombia, in the northern Andes (Fig. 6.10) is typical. The repeated oscillations in the relative abundance of the pollen of the three different species groups shown on Figs. 6.10 are a reflection of fluctuating climate. In cold epochs vegetation belts were depressed so that the site lay in paramo, high mountain moorland, in which grasses and the high mountain shrubs *Acaena* and *Polylepis* occur. By contrast, in Interglacials the tree line rose above the site and pollen of trees and shrubs predominated. Similar oscillations have been found in African and Malesian montane peat deposits, though none stretch so far back in time. Radiocarbon dating has shown that the oscillations were simultaneous at different places and also coincide with the alternating Glacials and Interglacials of temperate latitudes. The oscillations of the tree line in

all three tropical regions, reconstructed from numerous pollen profiles that have now been analysed, are shown in Fig. 6.11. The reduction in temperature during Glacial periods was greater at high elevations than in the lowlands and consequently vegetation zones were compressed and depressed (Fig. 6.12).

There are fewer records of changes in vegetation from the lowlands because suitable peat is uncommon and, although pollen in mineral soil can be used instead, few suitable pollen deposits have been found. Two profiles from the lowlands of northern South America are reproduced in Fig. 6.13. These show repeated oscillations between
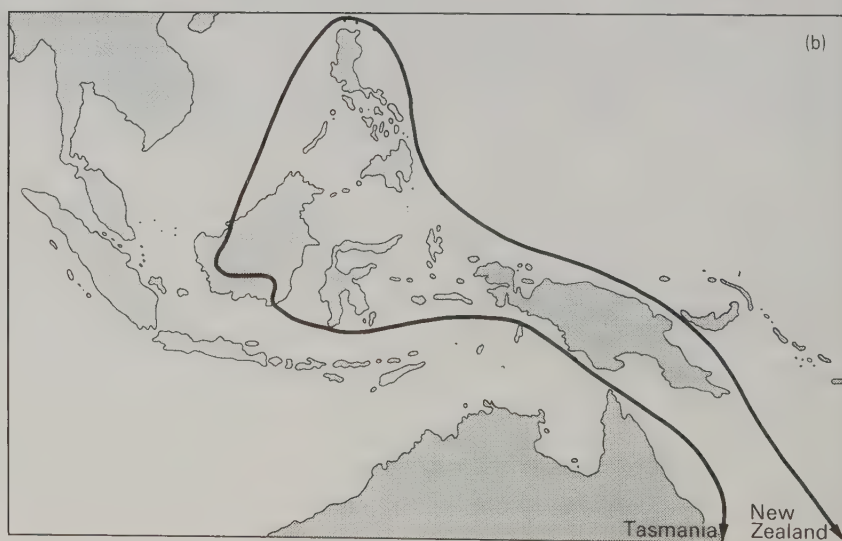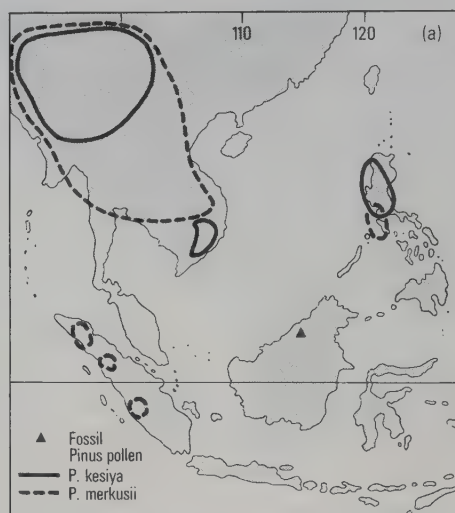
**Fig. 6.7.** In Malesia conifers have either a northern, Laurasian or a southern, Gondwanic centre of distribution (cf. Fig. 6.6). (a) *Pinus*, (b) *Phyllocladus*, celery pine. (Whitmore 1981, Figs. 8.1, 8.6.)
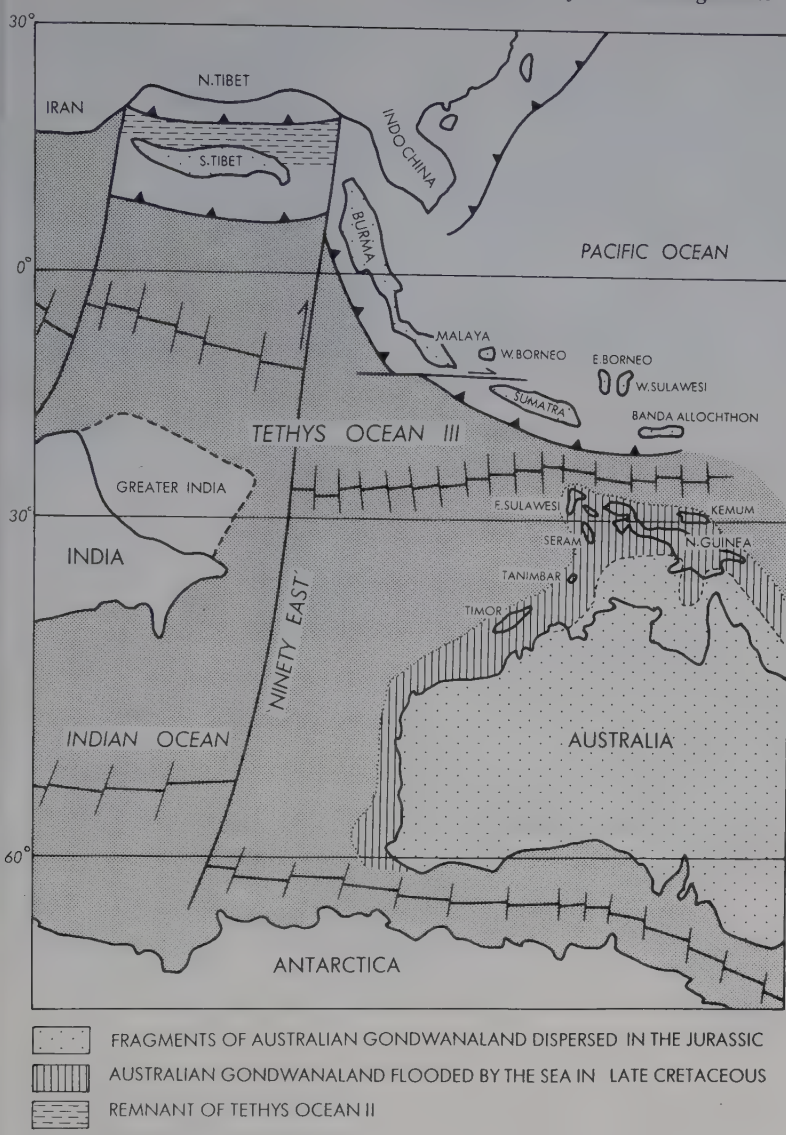
**Fig. 6.8.** Plate tectonics and the evolution of the Malay archipelago. In the late Cretaceous (90 million years ago) at the eastern end of the Tethys Ocean (cf. Fig. 6.1) fragments broke off northwest Australia and drifted northwards. (Audley-Charles in Whitmore 1987, Fig. 2.6.)

These 'stepping stones' possibly provided a migration route between Gondwanaland and Laurasia whose full implications for biogeography have not yet been analysed.

FRAGMENTS OF AUSTRALIAN GONDWANALAND DISPERSED IN THE JURASSIC
AUSTRALIAN GONDWANALAND FLOODED BY THE SEA IN LATE CRETACEOUS
REMNANT OF TETHYS OCEAN II

dominance by savanna herbs (including grasses) and by trees, which reflect drier and wetter conditions, respectively. Radiocarbon dates show that the oscillations correspond to Glacial and Interglacial periods. In central Malaya a mid-Pleistocene peat deposit below what is now the runway of Kuala Lumpur international airport was dominated by *Pinus* and grass pollen. Pine savanna is confined to strongly seasonal climates and is not found in Malaya today (Fig. 6.7a). At a site in lowland Amazonia pollen in riverine alluvial deposits shows repeated episodes of abundant grass at 4000, 2100, and 700 BP. This, however, prob-

ably reflects local variations in water level, hence in vegetation, and only indirectly indicates climatic fluctuation.

Cores from below the South China Sea between Malaya and Borneo, which are used by oil companies for stratigraphical analysis, include a horizon with abundant pollen of the conifers *Abies*, *Keteleeria*, *Pinus*, and *Tsuga*, and of the xeromorphic shrub *Ephedra*, all of which are today confined to much cooler, drier climates of continental Asia.

In the lowland rain forests of Queensland, pollen profiles have been described from peat de-
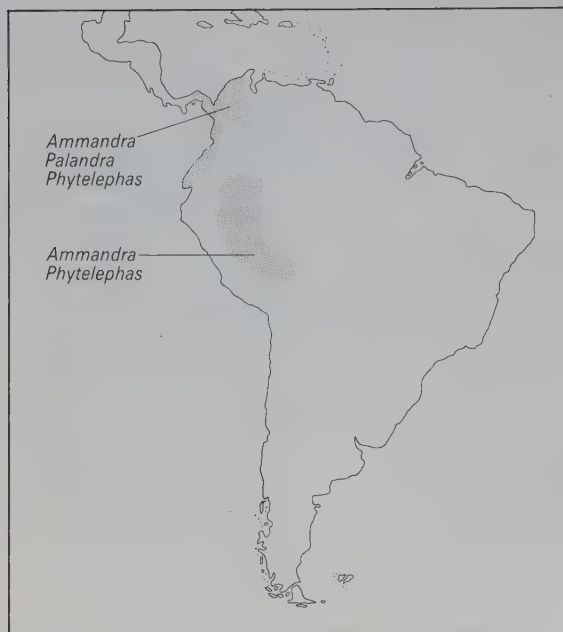
**Fig. 6.9.** The vegetable ivory palms, subfamily Phytelephantoideae, are confined to northwest South America where their range is disjunct. The uplift of the Andes, which continued to the end of the Pliocene 2 million years ago, split the range. Evolution continued. Today no species is found in the rain forests on both sides of the mountains. (After Uhl and Dransfield 1987.)

> Many groups show this pattern, with one set of species centred on the Choco region of Colombia the other in the Amazon, for example *Couepia, Licania,* and *Parinari* of the Chrysobalanaceae.



**Fig. 6.10.** Pollen diagram of a 200 m core of lake sediments and peat, extending for the whole Quaternary. Northern South America, at Bogota, Colombia, 2600 m altitude. (Data of van der Hammen in Flenley 1979, Fig. 4.12.)

> The repeated fluctuations in abundance of the three species groups is a reflection of continual climatic change.

posited in several volcanic crater lakes. Repeated oscillation between dominance by rain forest and by wet sclerophyll forest with much *Eucalyptus* (Fig. 2.6) has occurred. The present-day boundary between these two forest formations is only a few kilometres from the sites. Although there have undoubtedly been changes in vegetation these might be only slight and may not reflect more than small fluctuations in climate.

*Geoscientific evidence.* Previous seasonal climates in places that are at the present day perhumid can also be detected by physical signs. Soils containing true laterite, which only develop in seasonal climates with fluctuating soil water conditions, have been found below the South China Sea be-

tween Malaya and Borneo, part of the Sunda continental shelf. This sea-bed is also dissected by deep river valleys. On the Sahul shelf kunkar nodules, which similarly reflect a seasonal climate, have been found. The implication is that at Glacial maxima, when sea-level was lower and these continental shelves were exposed, the climate was indeed seasonal, as the pollen record indicates. Off the coast of South America sea-bed deposits also indicate past seasonal climate.

In northern South America sand dunes have been detected in the llanos savannas of Colombia, a region that today has a humid climate. The southern part of the Zaire rain forest of Africa grows over sands that have affinity with the Kalahari desert to the south. In both these regions the
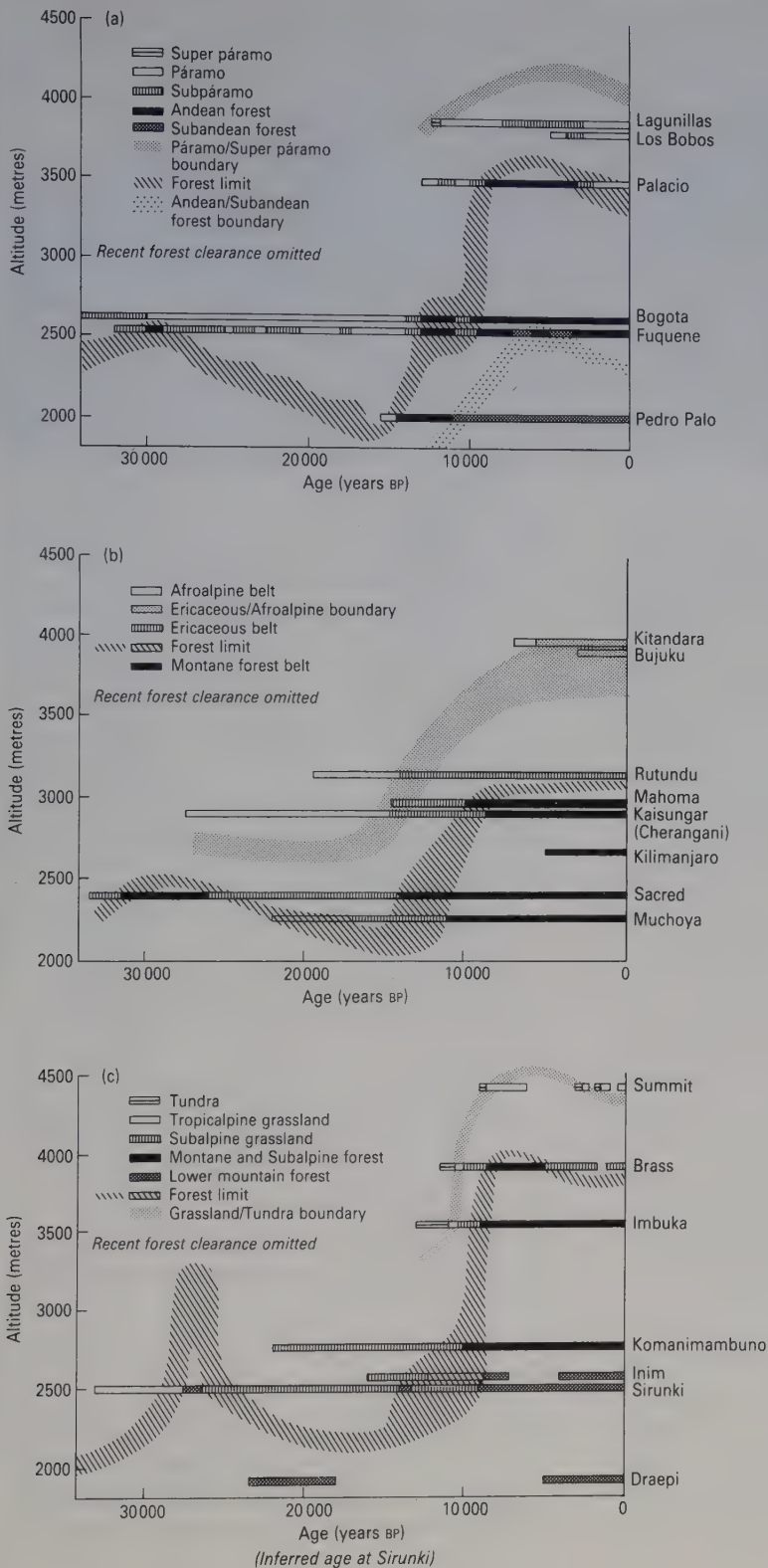
**Fig. 6.11.** Oscillations in the upper limit of forests during the late Quaternary in (a) the Colombian Andes, (b) the mountains of east Africa, and (c) the New Guinea highlands. (After Flenley 1979, Figs. 4.26, 3.24, 5.23.)

(a)

Altitude (metres)

Super páramo
Páramo
Subpáramo
Andean forest
Subandean forest
Páramo/Super páramo boundary
Forest limit
Andean/Subandean forest boundary

Recent forest clearance omitted

Lagunillas
Los Bobos
Palacio
Bogota
Fuquene
Pedro Palo

Age (years BP)

(b)

Altitude (metres)

Afroalpine belt
Ericaceous/Afroalpine boundary
Ericaceous belt
Forest limit
Montane forest belt

Recent forest clearance omitted

Kitandara
Bujuku
Rutundu
Mahoma
Kaisungar (Cherangani)
Kilimanjaro
Sacred
Muchoya

Age (years BP)

(c)

Altitude (metres)

Tundra
Tropicalpine grassland
Subalpine grassland
Montane and Subalpine forest
Lower mountain forest
Forest limit
Grassland/Tundra boundary

Recent forest clearance omitted

Summit
Brass
Imbuka
Komanimambuno
Inim
Sirunki
Draepi

Age (years BP)
(Inferred age at Sirunki)

**Fig. 6.12.** Vegetation zones on the Andes near Bogota, Colombia. Compared to (a) the present day, the zones were (b) both depressed and compressed at the last Glacial maximum. (After van der Hammen in Flenley 1979, Fig. 4.27.)

**Fig. 6.13.** Pollen diagrams from lowland northern South America (a) eastern Colombia and (b) Guyana. Radiocarbon dates are shown in years BP. (After Haffer in Whitmore and Prance 1987, Fig. 1.8.)

The repeated fluctuations in abundance of the three species groups shows an alternation between drier and wetter periods, with herbs and trees dominant respectively. The recent sharp decline in trees may reflect the influence of burning by Man.
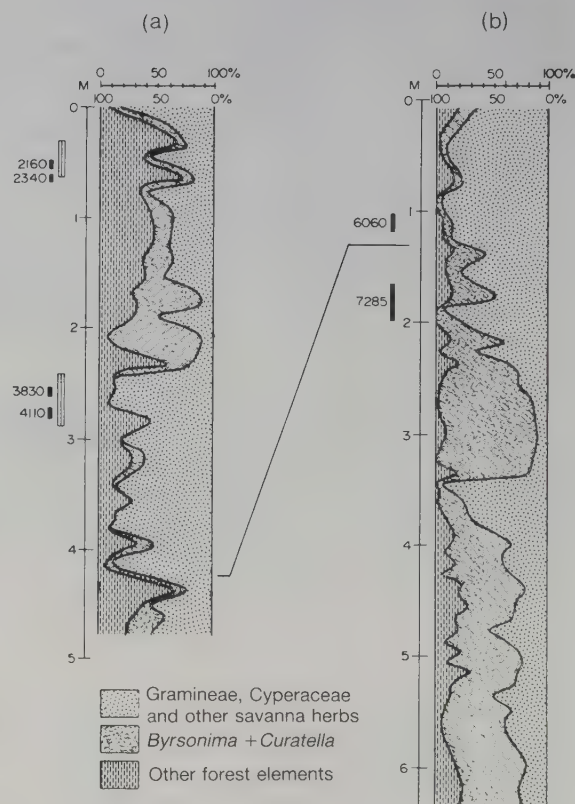
sand is thought to have blown on the wind and deposited in places that were open and very dry.

Land-forms provide further clues of past climate. Braided streams choked with debris develop in climates in which rivers flood during periodical wet seasons. Steep slopes form, surrounded by gentle plains with gravel beds, as periodic heavy rains erode the hills. In Amazonia, aerial survey has identified areas under rain forest today with these geomorphological signs that they developed in a seasonal climate. By contrast, in perhumid climates that do not have marked seasonality, rivers develop meanders, and hills are rounded and with deeper soils that are formed by chemical weathering and less mechanical erosion.[129]

Today the very highest equatorial mountains of New Guinea, East Africa, and the Andes have a permanent snow and ice cap, above *c.* 4500 m. During Glacial maxima the snow-line was depressed by as much as 1500 m (Fig. 6.12). Signs of glaciation can be seen today below the present snow-line and on some mountains that at present

have no snow-cap, for example Mt. Kinabalu, 4101 m, in northern Borneo was glaciated down to *c.* 3000 m (Fig. 6.14).

## The Tertiary

Less is known about Tertiary climates, that is before 2 million years ago. At least in the late Tertiary fluctuations similar to those of the Quaternary occurred. The pollen record near Bogota discus-

**Fig. 6.14.** The ice-smoothed rocky summit of Mt. Kinabalu, Sabah, 4101 m, which was covered by glaciers during the Quaternary ice ages.

sed above was truly remarkable in extending back 3.5 million years, during which period it recorded 27 complete climatic oscillations.[130] Earlier in the Tertiary the climatic gradient polewards from the Equator was less steep. For example, China was much warmer in the Miocene 5–24 million years ago than today. Tertiary climates have left their mark on present-day ranges of flowering plants in several ways.

There are 89 genera of flowering plants represented on both borders of the Pacific Ocean in both tropical America and tropical Asia (Figs.

5.1, 6.15).[131] These so-called 'amphiPacific tropical disjuncts' can hardly be explained by continental drift. They are in fact believed to have achieved their present range by migration northwards around the Pacific rim via the Bering Straits during warm parts of the Tertiary. This is substantiated by Tertiary fossil floras in Alaska which contain many subtropical and tropical plants, for example *Alangium*, *Cinnamomum*, *Firmiana*, *Macaranga*, and *Saurauia*.

Africa has a much poorer flora than the other two rain forest regions.[132] This is believed to be
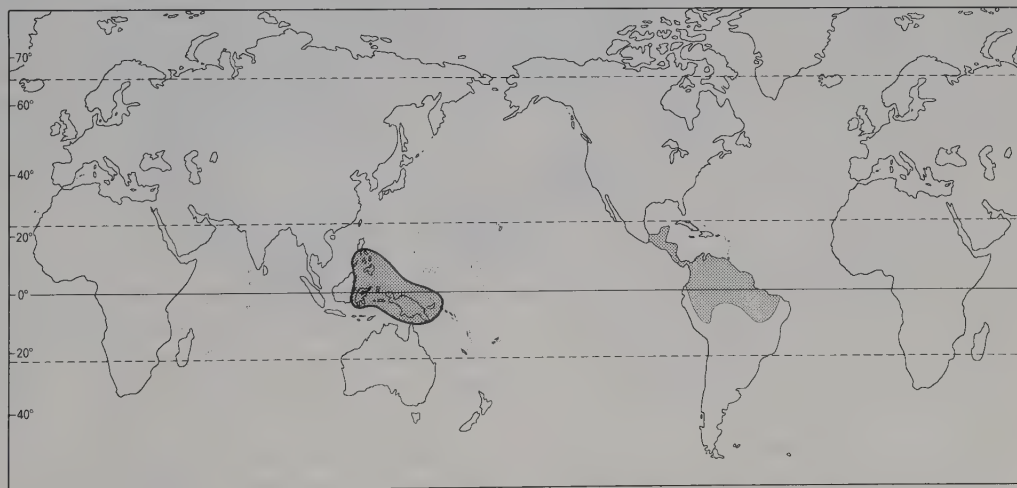


**Fig. 6.15.** The aroid genus *Spathiphyllum* occurs on both sides of the tropical Pacific Ocean as bole climbers in lowland rain forest.

Eighty-eight other genera show the same amphiPacific disjunction, including *Guettarda*, *Heliconia* (Fig. 5.1), *Saurauia*, *Sloanea*, and *Trigonobalanus*. (Map 5, van Steenis 1962).

because it was much more strongly desiccated during the Tertiary. We noted in Chapter 2 Africa's poverty in bamboos, ferns, and palms.

Australia too suffered strong Tertiary desiccation. At that time its mesic vegetation became mainly confined to the eastern seaboard. The strip of tropical rain forests found today in north Queensland is only 2–30 km wide and is of particular interest because it contains the relics of the old mesic flora. This includes the ancestors from which many modern Australian species adapted to hot dry climates are believed to have evolved, e.g. *Brachychiton*, *Flindersia*, *Gardenia*, in some cases by explosive speciation, e.g. *Acacia*. New Caledonia is a shard of Gondwanaland which drifted away eastwards from northeast Australia starting

in the Upper Cretaceous 82 million years ago. Because it is an island its vegetation has suffered less from the drier Glacial climates so more of the old flora has survived.

The lands bordering the western Pacific have the greatest concentration of primitive flowering plants found anywhere, including Amborellaceae, Austrobaileyaceae, Calycanthaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae, Lardizabalaceae, Magnoliaceae, Tetracentraceae, Trochodendraceae, and Winteraceae (Fig. 6.6c). It still remains debatable whether they survive here because conditions have been continuously favourable or occur here because this is where they evolved, i.e. their centre of origin. [133]

## 6.3. Pleistocene refugia[134]

The pollen record gives direct evidence for fluctuations in vegetation which reflect fluctuations in climate, and there are also various different clues in the physical environment from which the same climatic fluctuations can be deduced. It has been discovered that rain forests have waxed and waned in extent during the Quaternary, and probably in the Tertiary too, and are not the ancient and immutable bastions where life originated which populist writings still sometimes suggest. In the present Interglacial they are as extensive as they have ever been, or nearly so. At Glacial maxima lowland rain forests are believed to have contracted and only to have persisted in places where conditions remained favourable for them, as patches surrounded by tropical seasonal forests, like islands set in a sea. In subsequent Interglacials, as perhumid conditions returned, the rain forests expanded out of these patches, which have come to be called Pleistocene refugia.

In the late 1960s it was shown that within Amazonia birds have areas of high species endemism and richness which are surrounded by relatively poorer areas. The same was soon demonstrated for lizards. [135] Subsequently many groups of animals have been shown to exhibit such patchiness, notably butterflies, and so have flowering plants, though for them only a few families were included in the analysis. The centres of concentra-

tion more or less coincide with each other (Fig. 6.16a), and also with areas that geoscientific evidence suggests remained rain forested during drier Glacial times (Fig. 6.16b). The interpretation of these superimposed patterns is that rain forests have alternatively fragmented and expanded and that the centres of species richness and endemism are the places that have been continuously under rain forest. The hypothesis of Pleistocene refugia gains strength from the fact that many different groups of organisms all show similar patterns, especially at lower taxonomic levels. But forest fluctuations are undoubtedly only part explanation for patterns of distribution, just the last chapter in a long story of forces that have led to species differentiation.

In the African lowland rain forests there are three loci of species richness and endemism recognized by students of mammals, birds, reptiles, amphibians, butterflies, [136] and flowering plants. These are centred on Upper Guinea, on Cameroon and neighbouring Gabon, and on the eastern rim of the Zaire basin, respectively (Fig. 6.17). Tree species per hectare of over 0.1 m in diameter pick up this pattern. The Cameroon refuge had 138 species on the richest of several 0.64 ha sample plots at Korup and contrasted to less than 100 species per hectare for non-refugial sites in the African rain forests (Fig. 2.27). In Amazonia
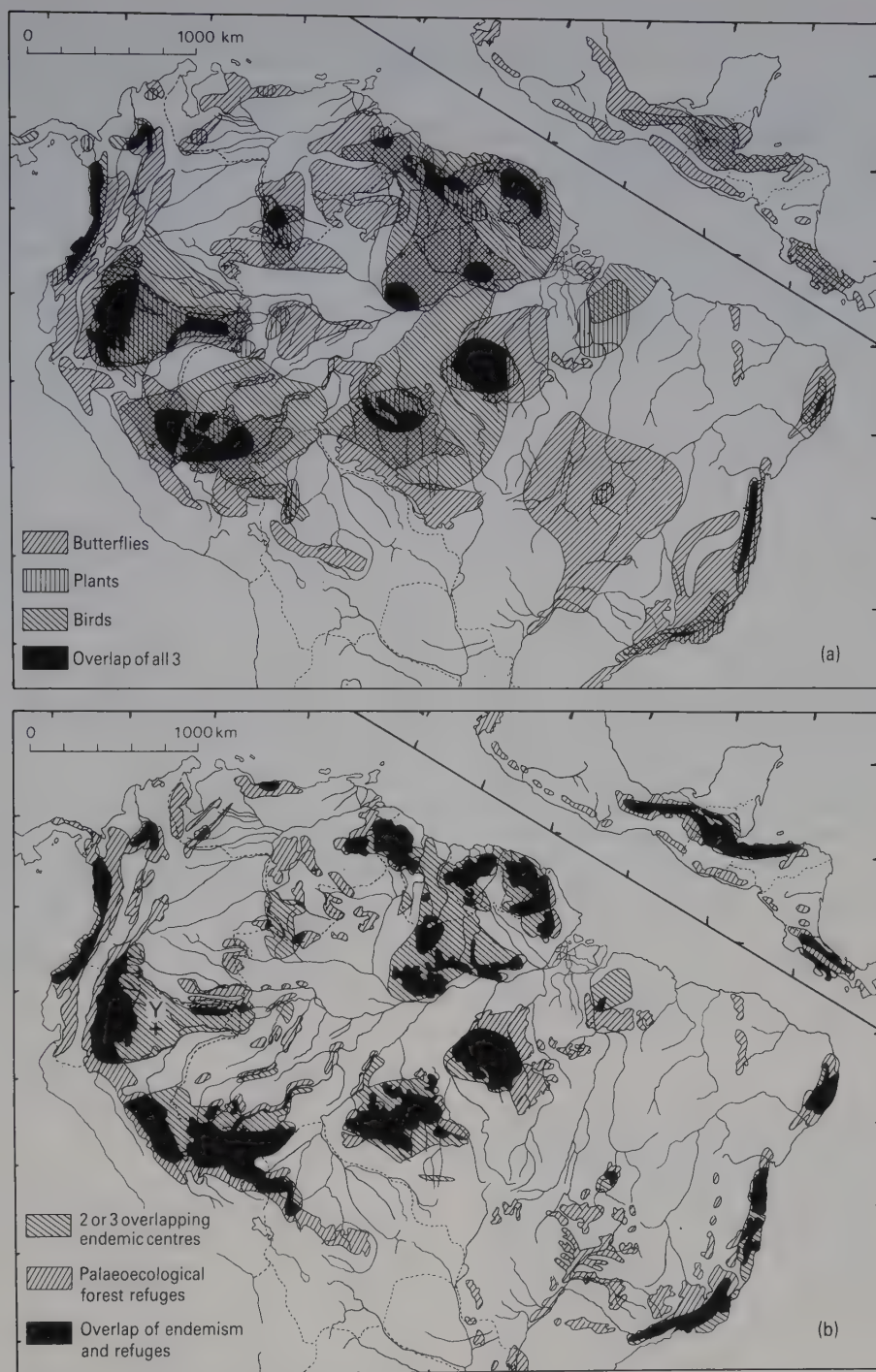
**Fig. 6.16.** Pleistocene refugia in the New World rain forests. (a) Centres of endemism of butterflies, plants, and birds. (b) The overlap of these with palaeoecological forest refuges as deduced from palaeoclimate, topography, geomorphology, soils, and vegetation structure. (Whitmore and Prance 1987, Figs. 7.4, 7.5.) Y is the Yanamomo site mentioned in Chapter 2.

The strong overlap within (a) and between this and the deduced palaeoecological refuges lends strength to the argument that Pleistocene refugia really existed.
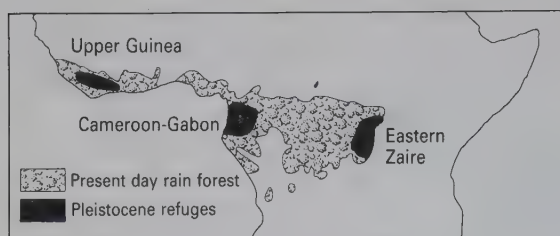
**Fig. 6.17.** Present-day extent of tropical rain forest in Africa. Areas of high species richness and endemism, which are postulated locations of Pleistocene forest refuges, also shown. (After Mayr and O'Hara 1986.)

hyper-richness has been found within the big Napo refuge in Peru, where the Amazon debouches from the Andes (see figs. 2.27, 2.28, 6.16a). There are not yet sufficient sample plots spread across Amazonia to confirm that tree species numbers on small plots reflect the pattern of refugia detected from other evidence.

All parts of Malesia are today about as equally rich in species, including endemics, as the Pleistocene refugia of Africa and America. At the Glacial maxima the Sunda and Sahul continental shelves were exposed by falling sea-level. Rain forests were likely to have become confined to the more mountainous places where there was more, orographic, rain. The main development of seasonal forests in this region is likely to have been on the newly exposed lowlands, and when sea-level rose again at the next Interglacial these and the physical signs of seasonal climates (described above) were drowned. The parts of Malesia that are above

sea-level today probably remained largely perhumid and covered by rain forest, which explains their extreme species richness and their lack of geoscientific evidence of seasonal past climates.

Present-day lowland rain forest communities consist of plant and animal species that have survived past climatic vicissitudes or have immigrated since the climate ameliorated. Thus many species coexist today as a result of historical chance, not because they co-evolved together. Their communities are neither immutable nor finely tuned. This point is of great importance to the ideas scientists have expressed concerning plant-animal interactions which were discussed in Chapter 5, as well as to theoretical discussions on the nature of plant communities.

Those parts of the world's tropical rain forests that are most rich in species are those that the evidence shows have been the most stable, where species have evolved and continued to accumulate with the passage of time without episodes of extinction caused by unfavourable climatic periods. This is similar to the pattern seen in other forest biomes, for example in the warm temperate forests of China[137] where there are species-rich patches with a concentration of relict conifers including the dawn redwood (*Metasequoia glyptostroboides*); and in the contrast between the species-rich Tertiary-relict Colchic forest at the eastern end of the Black Sea in Transcaucasian Russia with the rest of the European temperate broadleaf forest.

## 6.4. Seasonal climate elements in Malesia

Seasonal-climate plants in Malesia today have disjunct distributions, confined to continental Asia and Australia; their extents depend on how strongly seasonal a climate they require (Fig. 6.18), and on the two population areas being out of dispersal range of each other. In Glacial times when there was more seasonal forest, as described above, these ranges would have extended and become continuous or nearly so.

Elephant and gaur (*Elephas maximus, Bos gaurus*) today have races living in the rain forests

of western Malesia though they are mainly animals of the seasonal forests of continental Asia. Elephant browse on forest fringe and gap plants and gaur are commensal with shifting cultivators, inhabiting early regrowth forest on fallowed fields. It seems likely that these animals adapted to live in rain forest when their preferred seasonal vegetation disappeared as the climate ameliorated and sea-level rose.[138] The same may apply to the Sumatran rhinoceros (*Didermocerus sumatrensis*).

## 6.5. High mountain plants

A larger part of the land area of the humid tropics of Malesia is mountainous than is the case in Africa or America. European botanists living in Malesia, and perhaps nostalgic for home, have given much attention to the herbs and shrubs found above the tree-line. There are two floristic elements, one northern, epitomized by *Primula* and *Ranunculus* (primrose and buttercup), the other southern, e.g. *Gunnera* and *Nertera*.[139] At the present day, populations on different mountains are outside dispersal range of each other and of source areas in the Himalaya and Australasia. This no longer presents the enigma it formerly did, now it is realized that all

montane vegetation belts have been strongly and repeatedly depressed during Glacial maxima (cf. Fig. 6.12), with the consequence that populations would have been much closer. Mt. Kinabalu, the only really high mountain in Borneo, however, seems always to have been very isolated.[140] Nevertheless, it possesses a rich temperate flora (Fig. 6.19).

Patches of paramo moorland in the high Andes which are today widely separated islands would likewise have been closer together, if not continuous, at times in the past.



(a)

(b)

(c)
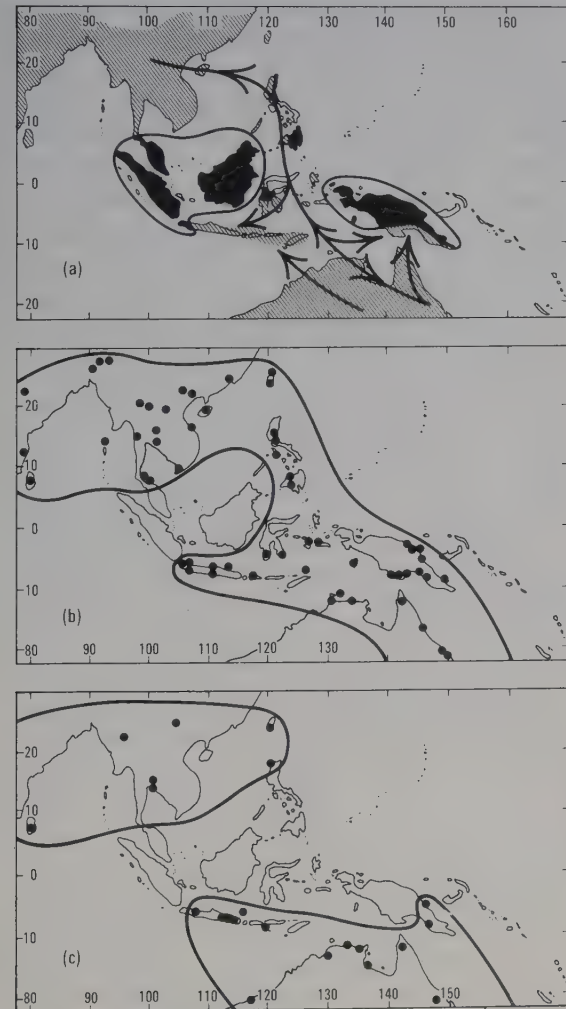
**Fig. 6.18.** Geographical ranges of two seasonal climate species in Malesia. (a) The two big cores of ever-wet rain forest as barriers for distribution of seasonal plants; the hatched areas either dry or consisting of a mosaic of ever-wet and dry areas. (b) *Pycnospora lutescens*, requiring some degree of dry season. (c) *Rhynchosia minima*, requiring a much stronger dry season; the disjunction is much more marked. (Fig. 14.4 in Whitmore 1984*a* after van Meeuwen, Nooteboom and van Steenis 1961.)

**Fig. 6.19.** *Coprosma hookeri* at 4000 m on Mt. Kinabalu, Sabah.

*Coprosma* is a genus of south temperate latitudes which extends into the tropics on high mountains.

## 6.6. Conservation

The central objective of rain forest conservation is to preserve adequate samples of the total diversity of species and ecosystems. Interactions between species and fluctuating climates on short, medium, and long time-scales are one motor of continuing evolution. The discovery that some rain forests have areas of high endemism provides criteria for the design of conservation areas. The biologist can state with conviction that it is necessary to include parts of these centres of endemism and of their boundaries, and also of surrounding species-poor forest, in order to conserve samples of the full diversity of the forest.

## 6.7.  Tropical rain forests through time—Chapter summary

1. In his search for generalizations the naturalist looks for repeating patterns of distribution and then for their interpretation. Two causes explain many patterns of tropical rain forest biogeography.

2. Continents have drifted. Some plants have ranges that arise from their occurrence on Gondwanaland and its fragments as these have moved apart (Fig. 6.1). Biogeography of the Eastern tropics (Figs. 6.5–6.7) reflects the convergence, then collision, of east Gondwanaland with Laurasia (Figs. 6.1, 6.8). Northern South American rain forest bigeography reflects the uplift of the Andes (Fig. 6.9).

3. Climatic history explains many other patterns. On the continental scale it explains some disjunct ranges, for example genera that occur in the lowland humid tropics on both sides of the Pacific (Fig. 6.15). Tropical climates have oscillated throughout the Quaternary, and at least the later Tertiary, between warm, wet periods, such as today, and cooler, drier, more seasonal periods. These correspond respectively to Interglacials and Glacials of high latitudes. Rain forests today are at or near their maximal extent. During Glacials their area was reduced and tropical seasonal forests became more extensive.

4. Evidence for fluctuating climates comes from two sources. Firstly, pollen analysis shows vegetation zones have fluctuated. Most data are from mountains and show vegetation types have moved up and down as climate has changed (Fig. 6.11). In parts of the lowlands, rain forest and more seasonal vegetation have alternated (Fig. 6.13). Secondly, direct physical evidence from geomorphology and soils, shows some rain forests occur today in places that once had seasonal climates.

5. In the neotropics many animals and some plants have areas of high species richness and endemism. These more or less coincide for different groups, and are believed to be Pleistocene refugia to which rain forest retreated at Glacial maxima, Geoscientific evidence for refugia is also more or less coincident (Fig. 6.16). In Africa there is evidence of three such refugia (Fig. 6.17).

6. Disjunct distributions of seasonal climate plants in Malesia (Fig. 6.18) and widely separated populations of high mountain plants would have been continuous or more nearly so in Glacial periods.

7. These patterns of distribution provide a rational basis for the design of conservation areas.

# Forest dynamics

In Chapter 6 tropical rain forests were examined on the long time-scale of tens of thousands of years and shown to have fluctuated in area. Delving further still, over millions of years, continental drift and evolution come into play. Present-day fauna and flora bear witness to these long-term changes. On these secular scales rain forests have been unstable and have changed profoundly in extent and composition, as indeed have all other biomes.

In the present chapter we look at temporal change at the other extreme, the lifespans of one or a few generations of trees. This we must examine in the context of the development and disintegration of the forest canopy, the forest growth cycle, introduced in section 2.3. We then go on to discuss silviculture, the way man makes use of forest dynamic processes to manipulate forest composition for his own benefit. Since about the mid 1970s investigations into the processes of forest regeneration and maintenance have been amongst the main interests of forest scientists in many parts of the world.[141] The processes described in rain forests in this chapter have close parallels elsewhere. There seems to be a general model of forest dynamics which holds in many different biomes, albeit with local variants. Ecology as a science is always seeking for generalizations to make sense of the bewildering diversity of Nature, and it appears that what is often called 'forest gap-phase dynamics' is one such generalization. This is a topic on which our understanding is currently advancing rapidly,[142] but as will be shown below, there remain important gaps in knowledge which are simply awaiting scientific attention.

## 7.1. Forest microclimates

The microclimate above the forest canopy, which is similar to that in a large clearing, is substantially different from that near the floor below mature phase forest. Figure 7.1 shows readings taken in the canopy at various heights above the ground. Outside, wind speeds during the day are higher, as is air temperature, while relative humidity is lower. Close to the ground within the forest, carbon dioxide content of the air remains high all the time but in the canopy it drops during the day due to uptake by photosynthesis.

The light climate within a forest is complex. There are four components, skylight coming through canopy holes, direct sunlight, seen as sunflecks on the forest floor, light transmitted through leaves, and light reflected from leaves, trunks, and other surfaces. The sky usually has some clouds and the first two components have approximately the same spectral composition. Light transmitted through, or reflected from, leaves is greenish because the orange to red wavelengths have been absorbed and utilized for photosynthesis (Fig. 7.2). The waveband 400 to 700 nm (which is approximately the visible spectrum) is utilized for photosynthesis and is known as photosynthetically active radiation or PAR. The forest floor only receives up to $c$. 2 per cent of the PAR incident on the forest canopy (Fig. 7.2), and 50–80 per cent of this is contained in sunflecks (Table 7.1). Plants living below closed forest probably rely almost if not wholly on the sunfleck component of the light climate for photosynthesis, the other components being too small to be utilizable. Compared to the open, most
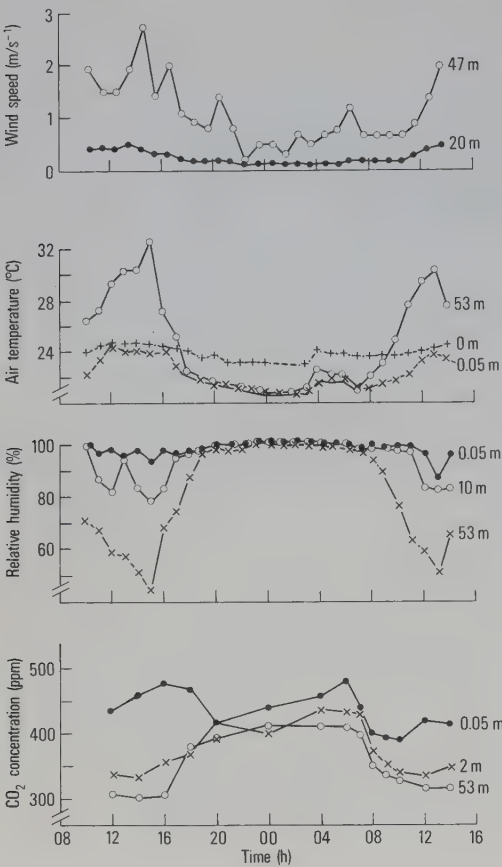
**Fig. 7.1.** The microclimate above the forest canopy strongly differs from that at ground level as is shown here by the daily march of wind speed, air temperature, relative humidity, and $CO_2$ concentration at various canopy levels in lowland rain forest at Pasoh, Malaya, 21–22 November 1973. (After Aoki, Yabuki and Koyama 1978, in Whitmore 1984*a*, Fig. 4.7.)

**Fig. 7.2.** The light in the open ('white light') and in deep forest canopy shade compared. There is a change in both quantity and quality. (Curves based on Fig. 1 in MacLellan and Frankland 1985.)
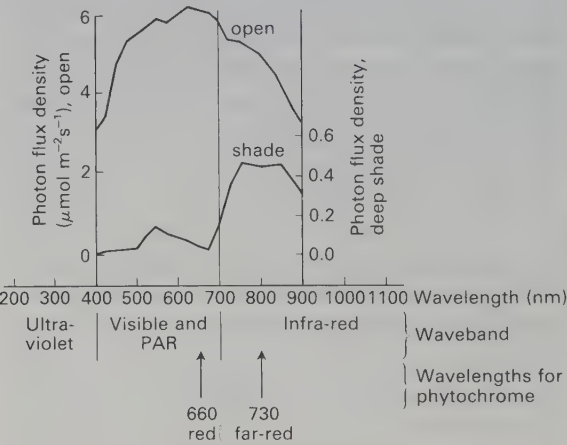


Table 7.1
*Forest floor light conditions*

| Location (latitude) | Mean per cent transmission PAR and range | Maximum % total PAR due to sunflecks |
|---|---|---|
| Queensland, Australia (28°15′S) | 0.5 (0.4–1.1) | 62 |
| Oahu, Hawaii (21°30′N) | 2.4 (1.5–3.8) | 80 |
| La Selva, Costa Rica (10°26′N) | *c.* 1.0–2.0 | 55–77 |
| Singapore (1°20′N) | *c.* 2.0 | *c.* 50 |

Mainly after Chazdon and Field (1984, Table 1).
Very little photosynthetically active radiation (PAR) penetrates the canopy and most of what does is contained in sunflecks.

sunflecks have low energy (Fig. 7.3). Very bright sunflecks are rare and may have more energy than shade-adapted leaves can utilize.

In addition to reduction in quantity of PAR within the forest canopy, PAR also changes in quality with a shift in the ratio of red to far-red wavelengths (660 and 730 nm) (Fig. 7.2). At La Selva, Costa Rica, the change was from a median value of the red/far-red ratio of about 1.2 in the open to 0.99 in sunflecks and 0.42 in forest shade. This is because the canopy preferentially absorbs the red waveband.

Canopy gaps have aerial microclimate like that above the forest but the smaller the gap the less different it is from the forest interior (Table 7.2, Fig. 7.4). In particular the amount of photosynthetically active radiation reduces (Table 7.1) and its distribution through the day alters. Both the quantity and quality of light reaching the plant is known to be of profound importance in the

(a) Forest floor

(b) 400 m² canopy gap

(c) 5000 m² clearing

Proportion (%) of ten-minute averages

PAR class ($\mu$mol m$^{-2}$ s$^{-1}$)

(b)
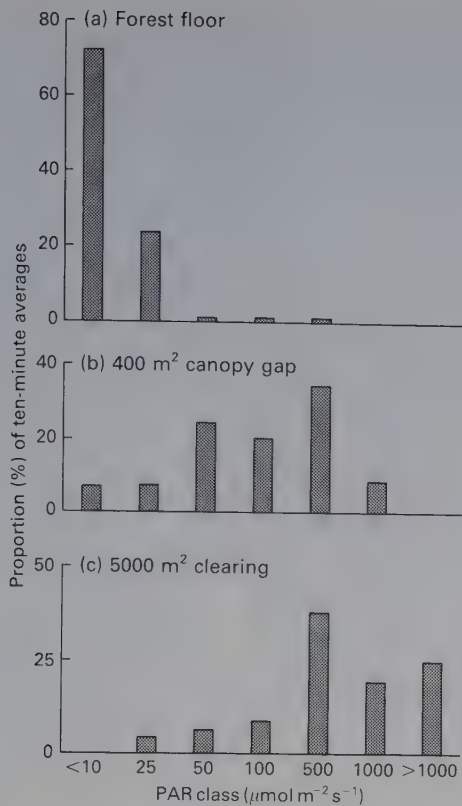
**Fig. 7.3.** Ten-minute average values of photosynthetically active radiation (PAR) at La Selva forest, Costa Rica. Inside the forest (a) most values are small with a few big ones due to sunflecks. In a canopy gap (b) values are larger, but less than in a large clearing (c). (After Chazdon and Field 1984, Fig. 2.)



(a)

(c)
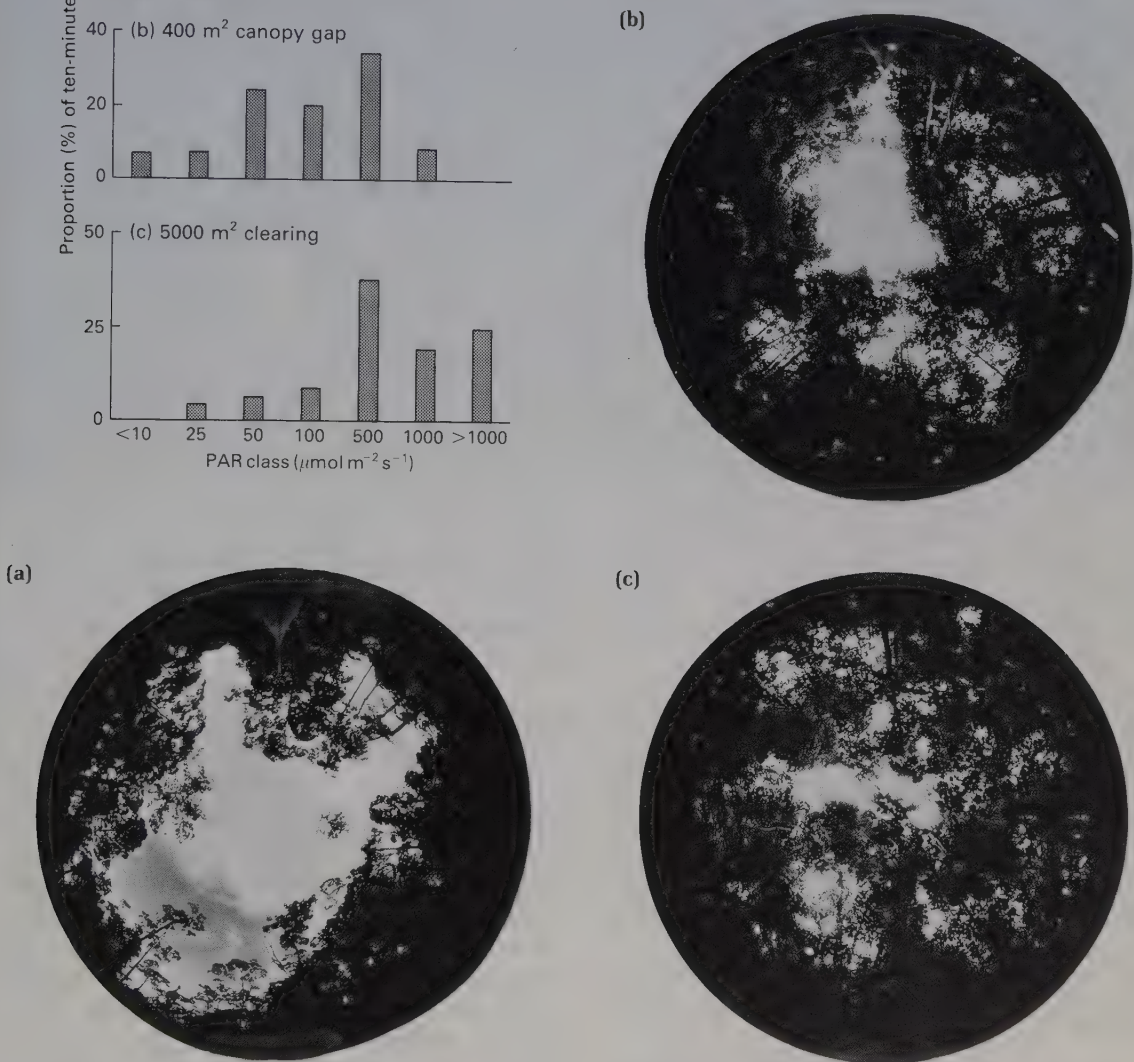
**Fig. 7.4.** Hemisphere photographs of (a) big gap, (b) small gap, and (c) closed mature phase canopy, with respectively 31, 10, and 6 per cent sky visible.

These are the sites in the Danum forest, Sabah, whose microclimates are shown in Table 7.2. Photographs taken with a 180° fish-eye lens. North at top. Sky percentage computed with an image analyser; the human eye is very deceptive. Note cloud in (a)

Table 7.2

*Microclimates of open, canopy gap, and closed lowland rain forest compared. (Danum, Sabah)*

|  | Open | Big gap | Small gap | Closed forest |
|---|---|---|---|---|
| Per cent sky visible[a] | 74 | 31 | 10 | 6 |
| Aerial microclimate: | | | | |
| Temperature, max./min. (°C)[b] | 30[c]/22.5 | 38/21.5 | 34.5/21.5 | 28.5/21 |
| Relative humidity, min. (%)[d] | 50 | 52 | 67 | 85 |
| Photosynthetically active radiation (mol m$^{-2}$day$^{-1}$)[e] | 35.0 | 19.2 | 4.9 | 0.5 |
| Soil mean temperature (°C): | | | | |
| 10 mm max./min. | 35.5/25 | 35/23 | 30.5/23 | 25/22.5 |
| 50 mm max./min. | 29.5/25.3 | 31.5/24.5 | 25.5/24 | 24.5/23.5 |

Unpublished data of N. Brown and D. Kennedy
The smaller the gap the more closely it resembles closed forest except that minimum temperatures are similar everywhere.
[a] Assessed from a hemisphere photograph (Fig. 7.4)
[b] Mean of weekly shaded value for 2 weeks every month for 12 months
[c] Open maximum temperature kept low by river breezes
[d] Mean daily value, from measurements of 2-week periods for 12 months
[e] Daily total, recorded 2 weeks every month for 12 months

mechanisms of gap-phase dynamics as will be shown later in this chapter. Due to the increase in solar radiation, the soil of gaps is more prone to drying out in rainless spells than soil below the canopy[143] and the temperature of the top few millimetres of soil may became as hot as 35 °C compared to only *c.* 25 °C below the canopy (Table 7.2). The manner in which different species are adapted to different dimensions of microclimate, especially the light climate, are still under exploration. Some of the important discoveries made so far are described below.

## 7.2. Pioneer and climax tree species[144]

In section 2.3 the different ecological classes of tree species were introduced. The grouping of trees into ecological species classes is one way the ecologist attempts to generalize and to detect recurrent patterns in the bewildering diversity of the forest.

### Pioneer tree species

Pioneer species germinate in a gap after its creation (Figs. 7.5–7.8). They grow fast in height (Fig. 7.8) and laggards are suppressed so the canopy grows up with a strong tendency to be one-layered. Below the canopy seedlings of climax species establish, and as the pioneer canopy breaks up through individual trees dying these climax species are 'released' (to use foresters' parlance) and grow up as a second growth cycle. Succession has occurred as a group of climax species replaces the group of pioneer species. Secondary tropical forests never have more than a small number of tree species per hectare, and may have only one or two, by contrast to primary forests which are usually very species rich.

Pioneer species are also called light-demanders or (shade-)intolerants with reference to their seedling requirements for solar radiation. Sometimes they are called secondary species because

**Fig. 7.5.** *Cecropia obtusa* (left) and *C. sciadophylla* (right). Brazilian Amazon.
*Cecropia* is the biggest genus of pioneer trees in the neotropics.

they form secondary or regrowth forest on cleared surfaces. The terminology is confusing, and there is no general agreement.

Amongst pioneers different species attain different heights at maturity, the larger ones being longer-lived. Table 7.3 lists common pioneer species from the different parts of the tropics. Reference is often made to small or short-lived and to big or long-lived pioneers, but it must be recognized that these are only arbitrary subdivisions of continuous variation. A big gap is sometimes simultaneously colonized by pioneers of different mature heights, for example in Central America *Cecropia, Ochroma* (balsa),[145] and *Trema* may colonize with *Cedrela*. To start with the small species dominate but as they die the bigger longer-lived pioneers come to dominate. Viewed from a roadside one sees two stages, early secondary (early seral) forests later turning into late

secondary (late seral) ones. Each has a different set of species dominant and succession seems to have occurred, but if one enters an early seral forest and makes an enumeration it is found that all the species colonized simultaneously and are present together throughout.

Pioneer species, as a class, have a whole syndrome of characters which fit them to their ecological niche. These are listed in Table 7.4 and discussed below. The group is defined on the first two characters, seed germination and seedling establishment behaviour, as the other characters are not always present.

### Climax tree species

Climax species usually germinate and establish below a canopy, therefore they can perpetuate *in situ*. They are sometimes called primary species

Table 7.3
*Some common rain forest pioneer tree species†*

| Stature | Neotropics | Africa | Eastern tropics |
|---|---|---|---|
| Small, 2–7.9 m tall | *Cordia nitida*<br>*Ocotea atirrensis*<br>Some *Piper*<br>*Vernonia patens*<br>*Vismia baccifera* | *Ficus capensis*<br>*Leea guineensis*<br>*Phyllanthus muellerianus*<br>*Rauvolfia vomitoria* | *Glochidion* spp.<br>many *Macaranga* spp.<br>some *Mallotus* spp.<br>*Phyllanthus* spp.<br>*Pipturus* spp.<br>*Trichospermum*, 8 spp. |
| Medium, 8–29 m tall | *Trema*<br>*Alchornea triplinervia*<br>*Cecropia*, 20 spp.<br>*Inga pezizifera*<br>*Jacaranda copaia*<br>*Ochroma lagopus*<br>*Protium glabrum* | *Trema*<br>*Anthocleista nobilis*<br>*Canthium arnoldianum*<br>*Cleistopholis patens*<br>*Macaranga*<br>*Maesopsis eminii*<br>*Musanga cecropioides*<br>*Spathodea campanulata*<br>*Vernonia conferta*<br>*Vismia guineensis* | *Trema*<br>*Acacia aulacocarpa*<br>*Acacia mangium*<br>*Adinandra dumosa*<br>*Alphitonia petrei*<br>*Anthocephalus*, 2 spp.<br>few *Macaranga* spp.<br>*Ploiarium alternifolium* |
| Large, >30 m tall | *Ceiba pentandra*<br>*Cedrela odorata*<br>*Cedrelinga*<br>*catenaeformis*<br>*Goupia glabra*<br>*Laetia procera*<br>*Swietenia* spp. | *Ceiba pentandra*<br>*Chlorophora excelsa*<br>*Chlorophora regia*<br>*Lophira alata*<br>*Nauclea diderrichii*<br>*Pericopsis elata*<br>*Ricinodendron heudelotti*<br>*Terminalia ivorensis*<br>*Terminalia superba* | *Eucalyptus deglupta*<br>*Paraserianthes* (*Albizia*) *falcataria* |

All the large and some of the medium sized species are important for timber
† African species from M. D. Swaine. American species from G. S. Hartshorn

or, with reference to their seedlings, (shade-) tolerants or shade-bearers. Climax is the term preferred here for this class of species. This is the group of which climax (primary) forest is composed, and climax plant communities are defined as those that are self-perpetuating, in a state of dynamic equilibrium. Seedlings below the forest canopy grow slowly, but in most species seldom reach taller than 1 m because they eventually die unless released.

Climax species may be subdivided in various ways, for example by usual mature height, but one of the most useful subdivisions is on the degree of seedling shade tolerance. At one extreme are climax species that are extremely shade-tolerant. These can establish and persist below very dense shade and need little extra solar radiation for release. The class includes those species of small trees that never reach the canopy top and probably only require enough growing space above and below ground to enable them slowly to attain maturity. Other species need a bit more solar radiation, a tiny canopy gap, for release. Strongly shade-tolerant species typically grow slowly and have dark, dense, hard and often siliceous timber which is often naturally durable. From this extreme there is a range of species with increasing light requirement, and at the other limit are climax species that need substantial solar radiation for release and growth (Figs. 7.9, 7.10). These grow faster and have paler, lighter, softer timber which is seldom siliceous and is seldom durable without

**Fig. 7.6.** *Macaranga gigantifolia*, aptly named from its huge leaves. East Kalimantan.



**Fig. 7.7.** *Macaranga triloba*. Malaya.

This genus ranges from West Africa to Polynesia. Most of its *c.* 250 species are pioneers which makes it easily the largest genus of pioneer trees in the world.

chemical preservation. The range of different sorts of climax species can often be found in a single forest (Table 7.5).

Climax species also have a whole syndrome of characters which fit them to their ecological niche. These are contrasted with those of pioneers in Table 7.4. The quintessential differences of climax species from pioneers are the abilities to germinate and to establish below a forest canopy, i.e. the first two characters of Table 7.4.

## Character syndromes of pioneer and climax species

It can be seen from Table 7.4 that in essence pioneer species are aggressive. They produce a large volume of low density wood (there are important exceptions, e.g. *Chlorophora excelsa*, iroko, of Africa, *Casuarina* and *Securinega* of the East) by fast growth, with open-branched crowns whereby they rapidly pre-empt competition by filling a large space. They start to reproduce early in life and produce copious seeds frequently, which are small and easily dispersed. By these means pioneers efficiently exploit new big gaps as these develop scattered through the forest. Growth is opportunistic and indeterminate, and continues so long as mineral nutrients and water are available. Leaves are short-lived and as their efficiency diminishes with age, their nutrients are recycled to fresh flushes so there is no great need to invest in mechanical (tough, fibrous leaves) or chemical protection against herbivores. Pioneers are unable

**Fig. 7.8**. *Ochroma lagopus*, balsa. A 3.5-year-old tree at La Selva, Costa Rica.

Most famous tropical pioneer tree species, widespread in the New World tropics, renowned for its very low density timber, where grown fast, which is much used for model-bulding and was formerly used for aircraft.

## Table 7.4
*The main characters of pioneer and climax tree species in tropical rain forests*

| | Pioneer | Climax |
|---|---|---|
| Common alternative names | Light-demander, (shade-) intolerant, secondary. | Shade-bearer, (shade-) intolerant, primary |
| Germination | Only in canopy gaps open to the sky which receive some full sunlight | Usually below canopy |
| Seedlings | Cannot survive below canopy in shade, never found there | Can survive below canopy, forming a 'seedling bank' |
| Seeds | Small, produced copiously and more or less continuously, and from early in life | Often large, not copious, often produced annually or less frequently and only on trees that have (almost) reached full height |
| Soil seed bank | Many species | Few species |
| Dispersal | By wind or animals, often for a considerable distance | By diverse means, including gravity, sometimes only a short distance |
| Dormancy | Capable of dormancy ('orthodox') commonly abundant in forest soil as a seed bank | Often with no capacity for dormancy ('recalcitrant'), seldom found in soil seed bank |
| Growth rate | Carbon fixation rate, unit leaf rate, and relative growth rates high | These rates lower |
| Compensation point | High | Low |
| Height growth | Fast | Often slow |
| Branching | Sparse, few orders | Often copious, often several orders |
| Growth periodicity | Indeterminate ('sylleptic'), no resting buds | Determinate (proleptic'), with resting buds |
| Leaf life | Short, one generation present, viz. high turn-over rate | Long, sometimes several generations present so slow turn-over rate |
| Herbivory | Leaves susceptible, soft, little chemical defence | Leaves sometimes less susceptible due to mechanical toughness or toxic chemicals |
| Wood | Usually pale, low density, not siliceous | Variable, pale to very dark, low to high density, sometimes siliceous |
| Ecological range | Wide | Sometimes narrow |
| Stand table | Negative | Positive |
| Longevity | Often short | Sometimes very long |

From Swaine and Whitmore (1988); Whitmore (1990)

to regenerate *in situ*, a mature stand has few small individuals, and the stand-table is negative (Fig. 7.11a).

Climax species, by contrast, are slower growing and with denser timber and denser crowns. In order to establish successfully below a canopy where photosynthetically active radiation is low, the seeds contain sufficient reserves for the seedling to build a root system and the first photo-synthetic organs. Seeds are fewer and larger, produced later and less often. There is not the imperative need for efficient dispersal over long distances because regeneration can occur below a canopy. Regeneration *in situ* means juveniles and adults usually occur together. In the jargon of foresters the stand-table is positive (Fig. 7.11b).

The least shade-tolerant climax species are very similar to pioneers except on the key properties of

**Fig. 7.9.** Pole of *Entandrophragma angolense*, a climax species whose seedlings grow fast in high solar radiation but soon die in deep shade. Ghana.



**Fig. 7.11.** Stand-tables of (a) the pioneer *Endospermum medullosum* and (b) the climax species *Parinari salomonensis.* Lowland rain forest, Kolombangara, Solomon Islands. (Whitmore 1974, Fig. 7.2.)

Pioneer species cannot reproduce within the forest canopy so the population consists mostly of big trees, whereas climax species reproduce *in situ* and have juveniles and adults present together and hence what foresters sometimes call a 'reverse J' or positive stand-table. See Figs. 2.22, 2.23.



**Fig. 7.10.** Pole of *Campnosperma auriculatum*, a climax species with similar high light requirements to *Entandrophragma* (Fig. 7.9). Malaya.

the capacity to germinate and establish below a canopy. Some foresters have recognized a group of 'late secondary species'. These are, in fact, either the long-lived pioneers described above or else this most light-demanding subgroup of climax species. Both these sets of species have as part of their character-syndrome rapid growth and pale, low density timber and many of them are very well-known to foresters as valuable timber producing species. 'Late secondary species' come from two quite distinct ecological classes with reference to regeneration requirements.

## Succession

The shift from a secondary forest of pioneers to a primary forest of climax species is sometimes called succession by 'relay floristics' by analogy to a race.[146] In some big gaps pioneer and climax species grow up together, the former from seed the latter either from seedlings which survived gap formation or from stem or root sucker shoots. In this case, which is likely where the forest floor has not been completely disrupted, succession is by simultaneous colonization, with the pioneers growing fastest and initially dominant. Both modes of succession can be found in the same forest, dependent on the severity of disturbance.

In a small gap, pre-existing climax seedlings are released. In a large gap pioneers which appear after gap creation form the next forest growth cycle. One of the puzzles that remains unsolved is what determines gap-switch size. Casual observations in western Malesia on dipterocarp seedlings show that in big gaps climax species become prone to attack by shoot borers or to partial defoliation or to leaf galls (Fig. 7.12). This suggests that the plants become stressed and unable to resist insect attack, and that in these conditions pioneers replace them. In Kramer's experiment, discussed in section 2.3, which was conducted in lower montane rain forest, gap-switch size was at between 1000 and 2000 m$^2$. In the lowlands where the climate is hotter and less humid pioneers are commonly observed in gaps above about 200 m$^2$. A specimen tree of the extremely shade-tolerant dipterocarp *Neobalanocarpus heimii* (chengal), a huge timber species, was planted in 1955 to celebrate the creation of Templer Park near Kuala Lumpur, Malaya. In this open site repeated shoot attack by boring insects has kept it the size of an apple tree, a sort of bonsai dipterocarp.



**Fig. 7.12.** Seedling of the dipterocarp *Parashorea malaanonan* in a big canopy gap with its apex destroyed by a shoot-borer and its leaves partially eaten. Sabah.

Table 7.5

*Regeneration behaviour of the common big tree species, Kolombangara, Solomon Islands*

| Group | Species | Conditions to establish | Conditions to grow up | Timber |
|---|---|---|---|---|
| Climax | *Dillenia salomonensis* | High forest | High forest | Heavy hardwoods: high density, hard, dark, often with silica |
| | *Maranthes corymbosa* | High forest | High forest | |
| | *Parinari salomonensis* | High forest | High forest | |
| | *Schizomeria serrata* | High forest | High forest | |
| | *Calophyllum kajewskii* | High forest/small gaps | High forest/small gaps | Medium hardwoods: medium density, hardness and colour |
| | *Calophyllum vitiense* | High forest | High forest/gaps | |
| | *Pometia pinnata* | High/disturbed forest | High forest/? small gap | |
| | *Elaeocarpus sphaericus* | High forest | Gaps | Light hardwoods: low density, soft, pale |
| | *Campnosperma brevipetiolatum* | High forest/gaps | Gaps | |
| | *Terminalia calamansanai* | High forest/gaps | Gaps | |
| Pioneer | *Endospermum medullosum* | Mostly gaps | Gaps | |
| | *Gmelina moluccana* | Mostly gaps | Gaps | |

From Whitmore (1974)
The degree of canopy disturbance needed for seedlings increases down the Table. Four ecological species groups can be recognised.

## 7.3. Seed and seedling ecology

**Pioneer species**

Pioneer species germinate from seed in a big gap after it forms. The seeds may be borne in after gap creation, or may already be present in the soil. C. F. Symington in 1933[147] reported that at Kepong, Malaya, he had placed some forest soil in the open and observed germination of pioneer species from it. The experiment was repeated by R. W. J. Keay in Nigeria in 1960[148] and many times again since the early 1970s in all parts of the tropics[149] with the same results: wherever a soil seed bank has been sought under lowland rain forest one has been found. Moreover, it is always mostly of pioneers.

Seed physiologists have discovered that pioneer species have seeds that can withstand desiccation and then become dormant; longevity is extended at low temperatures. They have called this behaviour 'orthodox'[150] (cf. Table 7.4). It is this capacity for dormancy that enables seeds to accumulate in the soil. However, beyond the demonstration that seed banks are (so far) ubiquitous little is yet known about their variation in either space or time. These are topics ripe for investigation. Pioneers have small, easily dispersed, copious seed, and the seed bank may develop by seed rain and be continually augmented. Experiments such as Symington's tell us nothing about how long seeds have been in the soil. In north Thailand the soil bank contained more seed than one year's production of nearby pioneers.

The alternative possibility is that the soil seed bank is a record or archive of pioneer trees that formerly occupied the site. Despite good adaptations to dispersal many seed are likely to fall below and near the parent tree. In this case the spatial pattern will be a series of patches or 'footprints'.

*Triggers to germinate.* The dormancy of the seeds of tropical pioneer species has been shown to be broken by one of two features of gap micro climate. Many, so-called photoblastic, species are triggered to germinate by exposure to light in which the energy of the red (660 nm) wavelength

exceeds the far-red (730 nm). This is mediated by their possession of the pigment phytochrome. Photoblastic germination is easy to demonstrate by experiment (see Fig. 7.13). Red light is depleted below a forest canopy by absorption and reflection (Fig. 7.2) and far-red exceeds red. The seeds have evolved to detect the occurrence above them of a canopy gap with full white light, in which red exceeds far-red. Moreover, short bursts of white light, as in passing sunflecks, do not trigger germination.

Other species, which include *Ochroma lagopus* (balsa), have seeds triggered to germinate by either high temperature, or by alternating high and low temperature. This so-called thermoblastic response enables them to detect the change from closed canopy to gap (Table 7.2). In parts of the neotropics pure extensive stands of balsa develop where burning has followed forest clearance. It has been discovered that *Ochroma* seeds have an impermeable layer in the testa which is ruptured by heat to allow the seeds to imbibe water and to germinate.

No other germination triggers have so far been detected for orthodox rain forest seeds. One
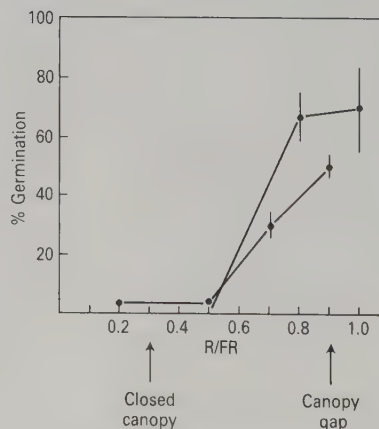


**Fig. 7.13.** The small pioneer tree *Urera caracasana* has photoblastic seeds which germinate at high ratios of red to far-red light (R/FR), i.e. in gaps, but not below the forest canopy. Los Tuxtlas, Mexico. (Orozco-Segovia *et al.* 1987, Fig. 1; the bars indicate standard errors.)

might expect germination in response to high irradiance or to a pulse of nitrate nitrogen, both known amongst temperate species. Like prolonged white light or high temperature, these cues are also both likely to be provided by gaps, in contrast to closed canopy. No one has yet looked very hard to see whether there are species that respond to these other cues.

*Microsite for establishment.* Soil seed stores characteristically contain many species. For example, small samples ($2\,m^2 \times 50\,mm$ deep) from six different forests in Ghana contained from 17 to 38 species each, nearly all of them pioneers. Equally characteristically, pioneer forests commonly comprise only one or a few tree species, and we do not yet fully understand why. Part of the answer probably lies in differential success in seedling establishment, dependent on weather at the time of germination, or on microsite. Table 7.6 shows results of an experiment in Venezuela where six of

the microsites commonly occurring in felled and burned forest were planted with six of the local pioneer species. The microsites differed substantially in soil surface temperature and water loss. Only one species, a forb (viz broadleaved herb), established on all six. Only the grass established on bare soil. All species except the grass established on the two microsites that were coolest and were moist.

## Climax species

Many rain forest climax species have seeds that germinate immediately or within a few days. They cannot withstand desiccation or low temperatures. These seeds have been called 'recalcitrant'[151] because they cannot be stored and thus pose a problem to plant breeders and nurserymen. Examples are many fruit species, e.g. citrus, mango, durian, and rambutan (*Citrus, Mangifera, Durio zibethinus, Nephelium lappaceum*) and many timber species including all rain forest dipterocarps. Not all climax species have recalcitrant seeds, for example many Leguminosae have hard testas and prolonged dormancy. No pioneer species has yet been found whose seeds are recalcitrant.

Climax species typically have bigger seeds than pioneers. By immediate germination they escape seed eaters and also degradation of their usually fatty storage tissues by micro-organisms. Seedlings develop, and climax species have a 'seedling bank' on the forest floor in contrast to the soil seed bank of pioneers.

### Table 7.6
*Different microsite preferences for establishment of six pioneer species in a cleared Venezuelan forest site*

| | Soil features | | Shrubs or trees | | | | Forbs | | Grass |
|---|---|---|---|---|---|---|---|---|---|
| | Maximum soil surface temperature (°C) | Mean water loss[a] | Cecropia ficifolia | Vismia lauriformis | Solanum stramonifolium | Clidemia sericea | Eupatorium cerasifolium | Borreria latifolia | Panicum laxum |
| **Without dead litter of leaves, twigs and branches:** | | | | | | | | | |
| Root mat | 50 | 8.9 | - | - | - | - | - | ★ | - |
| Charcoal | 54 | 6.9 | - | - | - | - | - | ★ | - |
| Bare soil[b] | 44 | 14.8 | - | - | - | - | - | ★ | ★ |
| **With litter** | | | | | | | | | |
| Root mat | 39 | 4.3 | - | - | - | - | - | ★ | - |
| Charcoal | c35 | 2.9 | ★ | ★ | ★ | ★ | ★ | ★ | - |
| Bare soil[b] | c35 | 6.7 | ★ | ★ | + | + | ★ | ★ | - |

Established success: ★ very good; + good; - weak or nil

[a]Water loss from a can of soil at field capacity in grams during an 8-h day

[b]Soil was a cream coloured sand

*Microsite for establishment.* As with pioneers, different climax species may be more successful on some parts of the forest floor. A close study of the seedling ecology of some Malayan Dipterocarpaceae by P. F. Burgess explained several previously enigmatic aspects of the distribution of this important family.[152] Dipterocarps are confined to the lowlands and do not penetrate lower montane rain forest. The upper limit was shown to be set by the inability of the radicle of a germinating seed to penetrate peat, which develops on the surface above 1050 m elevation. Seedling establishment is most successful on flat microsites; seedling stocking diminishes with increasing slope,

rapidly at microsites steeper than 45° and falling to nil at 65° slope. This explains the decrease in numbers of dipterocarps with elevation where the land becomes more rugged. The important timber species *Shorea curtisii* (seraya) was studied in detail. After the 1968 seed year seedlings were recruited markedly better on granite-derived soils, which are coarse and sandy, rather than on the more clay-rich soils derived from shale, probably because the latter develop a hard surface skin under the impact of heavy rain. However, after some years both sorts of soil had about the same stocking of seedlings; and the heavier mortality on granite-derived soils could be because their coarser structure makes them more prone to drought. This study serves to reveal the great complexity of intertwined factors that control seedling establishment and survival and are important in determining the ecological range of different species.

*Seedling survival.* Many seeds fall near the parent tree and dense carpets of seedlings form.

In several forests mortality has been shown to be density dependent, and therefore is greatest near the parent, presumably due to effects of pathogens or herbivores.[153] The few seeds that disperse to a greater distance are most likely to grow into seedlings that survive. This so-called 'escape hypothesis' has been invoked as a mechanism that prevents rain forest trees forming single-species stands, although there are exceptions. For the dipterocarps *Shorea leprosula* and *S. macroptera* it was found[154] that mortality depended more on microsite, and had no relationship to density or to distance from the parent. In the case of *S. curtisii* ants destroyed isolated seedlings, thus accentuating the clumping created by seed falling mainly near the parent.[155]

Dipterocarps bear fruit heavily only once every several years (p. 55). Seedling populations are then augmented and many attain a density of over one million per hectare. There is a subsequent decline, which may reach zero, before the next gregarious fruiting event (see Fig. 7.14).

## 7.4. Components of species richness

The dynamic nature of forest canopies provides many different regeneration niches to which different species have become specialized.[156] There are the broad major classes, pioneer and climax species, discussed above, which are specialized to large and small canopy gaps, respectively. These two classes are clear-cut with an easily observed or

tested, all-or-nothing, qualitative distinction between them. The numerous species within both classes are less easily classified, variation is continuous, and any subgroups are arbitrary.

In all tropical rain forest floras there are fewer pioneer than climax species, and they mostly belong to a few families; for trees these are Euphorbi-
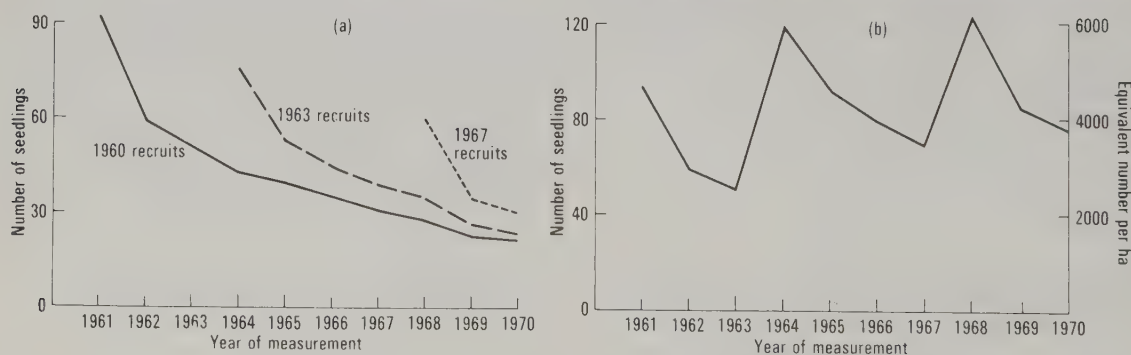


**Fig. 7.14.** Fluctuation of seedling populations of the light hardwood dipterocarp *Parashorea tomentella* at Sepilok, Sabah. (a) Fate of individual flushes; (b) total population. Numbers on eight plots of 4 × 10⁻⁴ha. (Fox 1972 in Whitmore 1984a, Fig. 7.7)

In Malaya, by contrast to Sabah, the populations of dipterocarp seedlings commonly drop to zero between successive flushes. This has important consequences for silviculture.

aceae, Malvaceae, Moraceae, Sterculiaceae, Tilia-
ceae, Ulmaceae, and Urticaceae. The Eastern tro-
pics are richest in pioneers, the biggest pioneer
genus, *Macaranga* (Euphorbiaceae; Figs. 7.6, 7.7),
is concentrated there though with a few outliers in
Africa. Most of its *c.* 250 species are pioneers and
many are confined to only one or a few islands of the
Malay archipelago. *Cecropia* (Urticaceae; Fig. 7.5)
is the second largest pioneer tree genus. It has only *c.*
20 species, most very widespread, and is entirely
neotropical. *Musanga cecropioides* (Urticaceae; Fig.
7.15) of Africa has similar crown form to these two.
It is monotypic. *Trema* (Ulmaceae), with 10–15
species, occurs in all three rain forest regions.
Pioneer genera do not have narrowly endemic
species of very restricted geographic distribution,
and most of them have only a few species. These
features are probably a reflection of efficient disper-
sal which militates against species evolution via the
development of localized genetically distinct popu-
lations. Moreover, some pioneers, including the
largest two genera *Cecropia* and *Macaranga*, are
dioecious, which has the same result. It is note-
worthy that the region with greatest numbers of
pioneer species is the Eastern tropics. This is prob-
ably because partial isolation on the islands that
comprise this region has allowed more species
evolution than has occurred on the continuous
landmasses of the African and American tropics.

There has been much speculation about the ex-
tent to which the coexistence of numerous species
in a given forest is due to specialization to differ-
ent facets of the regeneration niche, thus avoiding
direct competition. A little evidence has been
gathered. When a tree blows over its roots are up-
ended and a hollow is formed plus a mound of
mineral soil, sometimes called the root plate (Fig.
2.21). *Cecropia obtusa* in Guyana and *Trema
tomentosa* in Penang have been shown[157] to estab-
lish preferentially on root plates. It has also been
shown at La Selva that different species success-
fully establish seedlings in different parts of
treefall gaps, the crown, trunk, or butt regions.[158]

## Degrees of disturbance

The most species-rich forested landscape will be
one that includes patches of secondary forest re-
covering from a big disturbance and consisting of
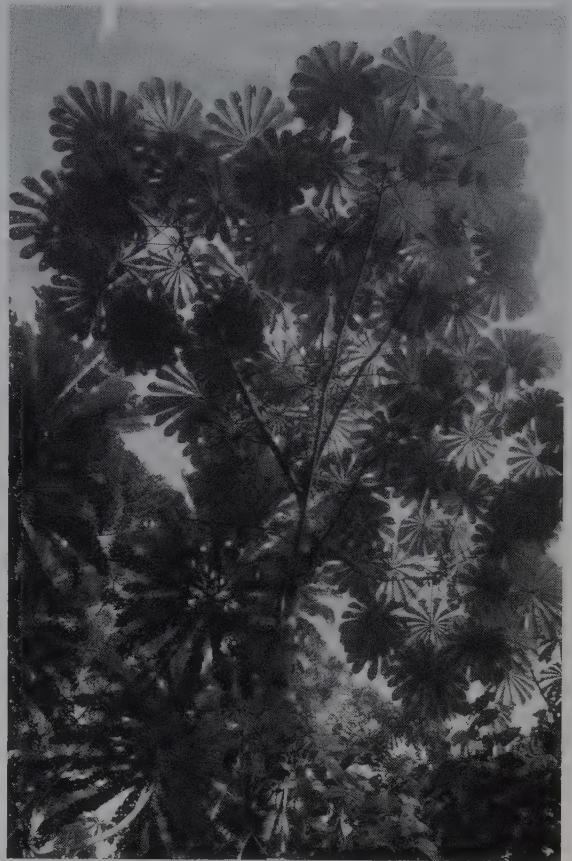


**Fig. 7.15.** *Musanga cecropioides* (palmate leaves) and
*Anthocleista nobilis* (oblong leaves), pioneers of West
African rain forests. Ghana.

pioneers, and patches of primary forest composed
of climax species. When succession is completed
and the whole landscape is primary forest again
there will be no pioneers and total floristic rich-
ness will be reduced. This is the *intermediate dis-
turbance hypothesis* of J. H. Connell;[159] the rather
obvious statement that the most species-rich com-
munity is that at an intermediate stage in recovery
from disturbance and therefore containing both
pioneer and climax species. The concept is bound
to be true at certain scales of dimension, but if we
were to look at tiny patches of the landscape we
would probably find species-poor stands of
pioneers and also stands of high species richness
where the more numerous climax species occur in
greater mixture and which have, moreover, accu-
mulated dependent synusiae of epiphytes and
climbers, so at this scale the climax patches are

richest. The catch-all hypothesis of Connell included intermediate intensity and frequency of disturbance as well as intermediate stage of recovery. It caused scientists to look at species composition

in a particular way, but is not so much an hypothesis as an inevitable property of vegetation at certain scales of space and time.

## 7.5. Growth and shade tolerance analysed

The physiological basis of growth rates and of shade tolerance amongst tropical rain forest tree species until recently remained unknown. Over the last few years robust, portable, battery-powered equipment based on microelectronics has become available and scientists are now beginning to address these very basic questions. This is the interface between ecology and physiology, so-called ecophysiology. Experiments in the laboratory are at best of only limited relevance, and very rapid developments and exciting discoveries are now being made by working in the forest.

The basis for the fast growth of pioneer trees is their high unit leaf rate, E, the rate of dry weight created by photosynthesis per unit area of leaf. Table 7.7 shows that of six species studied at La

Selva, Costa Rica, *Ochroma lagopus* (balsa) had unit leaf rate not significantly lower than that of the herb *Helianthus annuus* (sunflower) grown as a control. Other species, subjectively ranked as progressively more shade-tolerant, had progressively lower unit leaf rate. Relative growth rate (dry weight increase per unit of dry weight) also decreased with increasing shade tolerance but is a less basic measure because it changes with age. Other research has shown that the rate of carbon dioxide uptake is also higher in light-demanding than in shade-tolerant species, despite high variability due to leaf age and past history (Fig. 7.16).

Within the forest most of the photosynthetically active radiation (PAR) is in the sunflecks (section 7.1). Recent research[160] on the herb *Alocasia*

Table 7.7

*Growth in an open site expressed as unit leaf rate (E) and relative growth rate (RGR) of seedlings of six tree species of increasing shade tolerance compared to sunflower,* Helianthus annus. *(*La Selva, Costa Rica*)*

|  |  | E $(g\,m^{-2}\,week^{-1})$ | E as % of *Helianthus* | RGR $(g\,g^{-1}\,week^{-1})$ |
|---|---|---|---|---|
| *Helianthus annuus* | (i) | $57^a$ |  | 1.00 |
|  | (ii) | $65^a$ |  | 0.75 |
| Pioneer species |  |  |  |  |
| *Ochroma lagopus* | (i) | $57^a$ | 87% | 0.85 |
|  | (ii) | $52^{ab}$ | 79% | 0.81 |
| *Heliocarpus appendiculatus* |  | $42^b$ | 65% | 0.54 |
| Climax species 'Gap-dependent spp.' |  |  |  |  |
| *Cordia alliodora* |  | $41^b$ | 64% | 0.48 |
| *Terminalia oblonga* |  | $10^c$ | 15% | 0.13 |
| 'Shade-tolerant canopy spp.' |  |  |  |  |
| *Brosimum alicastrum* |  | $26^{bc}$ | 40% | 0.15 |
| *Pentaclethra macroloba* |  | $22^c$ | 34% | 0.15 |

From Oberbauer and Donnelly (1986, Table 2)
[a,b,c] Different letters following E show significantly different values
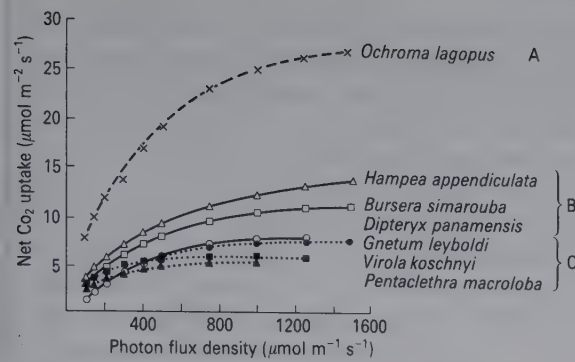
**Fig. 7.16.** Photosynthesis rate of seven tree species at La Selva, Costa Rica. A, Pioneer: B, gap-dependent; C, shade-tolerant canopy species. (After Oberbauer and Strain 1984, Fig. 1.)

Rate of photosynthesis (measured as net $CO_2$ uptake) increases to an asymptote with increasing light. The maximum decreases with increasing species shade tolerance.

*macrorrhiza* and on seedlings of the tree *Toona australis*, both shade-tolerant species from the Australian rain forests, showed that photosynthesis took 25–40 minutes to reach steady state in bright light after a prolonged, low light period. That is to say there is an induction period. For *Alocasia* loss of induction when the plants were put back into low light conditions took over 60 minutes. Furthermore, the rate of carbon gain varied with past history and intermittent sunflecks could be used more efficiently than continuous high light. The conclusion is that the temporal pattern of sunfleck distribution through the day (cf. Fig. 7.3) is of importance, not just the daily total PAR. Further studies like this are needed to analyse interspecific differences of shade tolerance.

Shade tolerance itself is a property that awaits close analysis. There are several possible aspects. We do not yet know whether different climax species known subjectively by foresters to have different tolerance either (i) establish seedlings at different levels of PAR, or (ii) have differential longevity at a given level of PAR, or (iii) require a different extra amount of PAR for release. Only experiments will tell.

Studies in the Pasoh forest, Malaya, on mixed populations of seedlings of the dipterocarps *Shorea leprosula* and *S.maxwelliana*, the latter much more shade-tolerant, showed 27 and 167 per cent annual mortality, respectively.[161] The more shade-tolerant *S.maxwelliana* survived better over the 2-year study period. Herbivorous insects removed 13 and 5 per cent of the leaf area, respectively. However, artificial removal of 25 per cent of leaf area did not significantly alter rates of mortality, suggesting that the survival difference was in fact not due to herbivory.

Mean rates of respiration and photosynthesis of different ecological species groups are shown in Table 7.8. Such measurements are very difficult to make or interpret because rates are dependent on so many variables, such as leaf age, past history, and orientation, which makes different studies hard to compare. Moreover, an individual may change as it grows. The general pattern is that understorey species differ from the others in

Table 7.8

*Mean rates of respiration and photosynthesis of ecological groups of rain forest species*

| Authors' groups | Early successional trees | Canopy trees | Understorey plants |
|---|---|---|---|
| Probable equivalent groups | Pioneer spp. | Light-demanding climax spp. | Shade-tolerant climax spp. |
| Photosynthesis (mg $Co_2$ $dm^{-2}$ $h^{-1}$) | 14.1 | 6.9 | 2.9 |
| Respiration (mg $Co_2$ $dm^{-2}$ $h^{-1}$) | 2.0 | 1.0 | 0.3 |
| Respiration as % photosynthesis | 14% | 15% | 10% |

From Bazzaz and Pickett (1980)

that their respiration is only *c.* 10 per cent of photosynthesis instead of *c.* 15 per cent; thus they respire relatively less and this is part of their means of shade tolerance. It is interesting in this respect that both species of dipterocarp seedlings

in the Pasoh study had similar total starch contents. After total defoliation *S.maxwelliana* seedlings died more slowly, which is probably an indication of a lower respiration rate in this more shade-tolerant species.

## 7.6. Disturbance regimes

Some parts of the humid tropics are much more prone than others to extensive, catastrophic disturbance. The two belts of latitude where cyclones are common were mentioned in section 2.3. A coarse-scale structural mosaic of the forest and the abundance of big-gap species betoken such disturbance.

### Papua New Guinea

This is a land wracked by continual catastrophe.[162] The mountains are young and continuing to uplift as the Australian plate subducts below the Pacific plate (see Chapter 6), so earthquakes with associated landslides are frequent on the young steep slopes. There are numerous active volcanoes which create lava flows and mudflows (lahars) and thick ash deposits. Strong destructive winds occasionally occur. In exceptionally dry years those forests that are always slightly seasonal become unusually dry and may catch fire. The big rivers which run on to the coastal plains have unstable courses. Shifting cultivation and associated regrowth forest (cf. section 8.1) is

also extensive. It is no surprise that lists of timber tree species for a tract of lowland rain forest in Papua New Guinea usually include a considerable proportion of pioneers, such as species of *Albizia*, *Paraserianthes* and *Serianthes*, or *Eucalyptus deglupta*, besides strongly light-demanding climax species such as *Campnosperma* spp., *Pometia pinnata*, and *Terminalia* spp.

### Peru

Aerial photographs or satellite images of Amazonian Peru reveal curious and conspicuous stripes in the forest canopy. Ground inspection shows these stripes represent forests of different species composition.[163] The upper tributaries of the Amazon which traverse the region run rapidly off the slopes of the Andes and are subject to violent annual flooding. They have a high silt load. Every year they change course, easily eroding the soft alluvial river banks, and move laterally many metres, in one case 180 m. Fresh alluvial banks are created on which primary succession occurs (Fig. 7.17). The stripes seen from the air are different stages
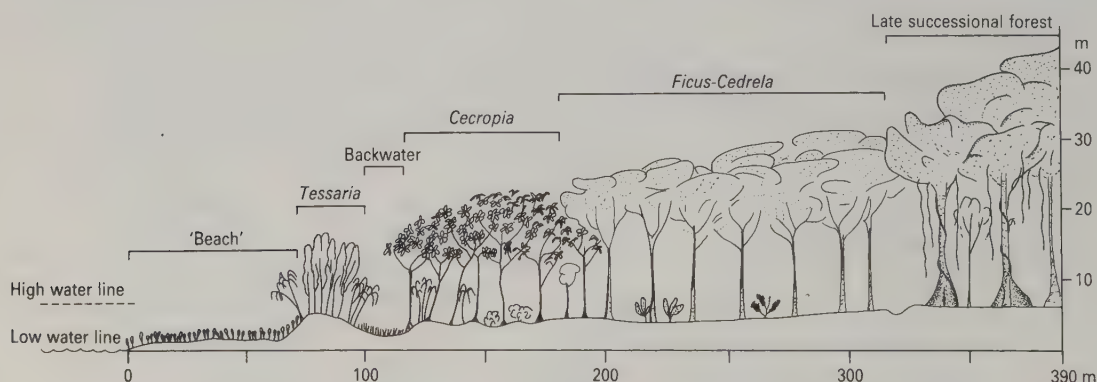


**Fig. 7.17.** Primary succession on newly deposited riverine alluvium, at Cocha Cashu on the Rio Manu in Peruvian Amazonia. (Salo *et al.* 1986, Fig. 3.)

of this succession. Climax is never reached, a new flood always intervenes to destroy the forest. Over a quarter of the Peruvian Amazon forests show these characteristics. The disturbance creates a mosaic of forest facies with strong species diversity between them; this is diversity from place to place within the same community and is sometimes called beta diversity (cf. section 2.4). The only other place where this pattern has been discovered is in much smaller areas of Papua New Guinea, as already mentioned, (Fig. 7.18).

### Drought and fire

Between July 1982 and April 1983 east Kalimantan received only 32 per cent of its usual 1820 mm of rain (Fig. 7.19). This was part of a pantropical climatic perturbation, called the El Niño Southern Oscillation, which resulted from anomalous warming of the usually cool surface of the eastern equatorial Pacific Ocean.[164] In early 1983 fires started and burned for many months. In total over three million hectares of lowland rain forest were destroyed in Kalimantan and over one million

more further north in Sabah.[165] Subsequent investigations revealed that in Sabah 85 per cent and in Kalimantan about a third of the forest destroyed had been recently logged, and would have had a lot of readily flammable dry dead wood. Only about a third ($1.35 \times 10^6$ ha) of the destroyed Kalimantan forest was primary and part of that ($1 \times 10^5$ ha) was killed by drought not by fire: the big trees, especially dipterocarps, had been singularly susceptible.[166] Research into the climatic record revealed that similar droughts have occurred in eastern Borneo two or three times in the last century. The still grass-covered 80 000 ha Sook Plain of Sabah originated from a fire in 1915 after an exceptionally dry period. The affected area of Kalimantan had previously been almost uninhabited. Immigrant Buginese settlers from Sulawesi had recently moved in illegally along newly built timber extraction roads. When the drought occurred fire escaped from their fields and set light to the dead trash left behind after lumber extraction. It appears eastern Borneo has always been susceptible to rare droughts associated with El Niño events. The difference was that in 1982 human activity dramatically exacerbated the consequences. During the same period huge fires in the peat swamp forests of east Sumatra created such a dense smoke haze in Singapore, over 150 km away, that the airport was closed.

The same El Niño event caused an exceptionally strong dry season in Panama and on a permament



**Fig. 7.18.** Primary succession on an accreting river bank, south Papuan coast. Swamp grassland is replaced by a narrow belt of the pioneer tree *Octomeles sumatrana* as the levée builds up. On the right climax species have grown up under the *Octomeles* which persists as big scattered individuals.
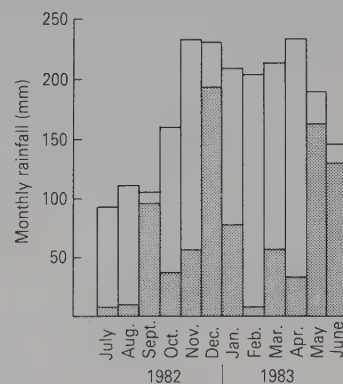


**Fig. 7.19.** The 1982–1983 drought in northeast Borneo. Long-term mean monthly rainfall, and 1982–1983 rainfall (shaded) at Kota Bangun, Kalimantan. (Lennertz and Panzer 1983, Fig. 1.)

sample plot of 50 ha on Barro Colorado Island un-usually high tree mortality occurred.[167]

The Great Fire of Borneo was unexpected (although in fact it was mainly freshly logged forest that burned) because until recently it had been believed that primary rain forest, in contrast to secondary regrowth, is not flammable. This view was also challenged by the discovery in the early 1980s of charcoal in the soil under rain forest in the north central Amazon basin.[168] [14]Carbon dates show numerous fires have occurred since 6260 BP, the mid-Holocene, and up to a few hun-dred years ago. Some of them coincide with known dry phases. More recently charcoal has been found in several places below the Brazilian Amazon rain forests.[169]

These occasional or rare catastrophic events leave their mark on the forest perhaps for a century or more (Fig. 7.20). They can be more critical to the forest than average conditions: an instance when 'extremes are more important than means'. Another nail is thus driven into the coffin of the supposition that tropical rain forests are ancient and immutable, and one is led to speculate to what extent contemporary human perturbation might soon lead to spectacular forest destruction (cf. section 10.5).

## 7.7.  Silviculture

Rain forest silviculture is the manipulation of the forest to favour certain species and thereby to en-hance its value to man. For example, around the turn of the twentieth century the Malayan rain forest was treated to increase the abundance of *Palaquium gutta* (Sapotaceae) because there was a strong market for its latex, gutta-percha, which was used as the insulator in submarine telegraph cables.[170] More commonly, manipulation is to favour particular timber species. Timber prop-erties, whether heavy or light, dark or pale, dur-able or not, are strongly correlated with growth rate and thus to the extent to which the species is light-demanding (Table 7.5). Thus, the ecological basis of natural forest silviculture is the manipula-tion of the forest canopy. The biological principle of silviculture is that by controlling canopy gap size it is possible to influence species composition of the next growth cycle. The bigger the gaps the more fast-growing light-demanders will be favoured. This concept has been known in con-tinental Europe since at least the twelfth century. Indeed, our knowledge of forest dynamics, the forest growth cycle, and the significance of canopy gap size, was discovered by foresters empirically before the formal science of ecology came into existence.[171] The practice of silviculture reached tropical rain forests via India and Burma then Malaya and was strongly influenced by teutonic tradition.

### Silvicultural systems

The silvicultural systems that have been applied to tropical rain forests belong to one of two kinds, the polycyclic and monocyclic systems, respect-ively (Figs. 7.21–7.23). As the name implies, polycyclic systems are based on the repeated re-moval of selected trees in a continuing series of felling cycles, whose length is less than the time it takes the trees to mature (which foresters call the rotation age). The aim is to remove trees before they begin to stagnate and deteriorate from old age, leaving all appreciating stems to swell the future yield. Because of the very species-rich nature of most tropical rain forests, and the relat-ively small number of species with timber that is commercial by current standards, extraction on a polycyclic system tends to result in the formation of scattered small gaps in the forest canopy.

By contrast, monocyclic systems remove all saleable trees at a single operation, and the length of the cycle more or less equals the rotation age of the trees. Except in those cases where there are few saleable trees, damage to the forest is more drastic than under a polycyclic system, the canopy is more extensively destroyed, and bigger gaps are formed.

It can be seen at once that the two kinds of sys-tem will tend to favour shade-bearing and light-demanding species, respectively, but the extent of
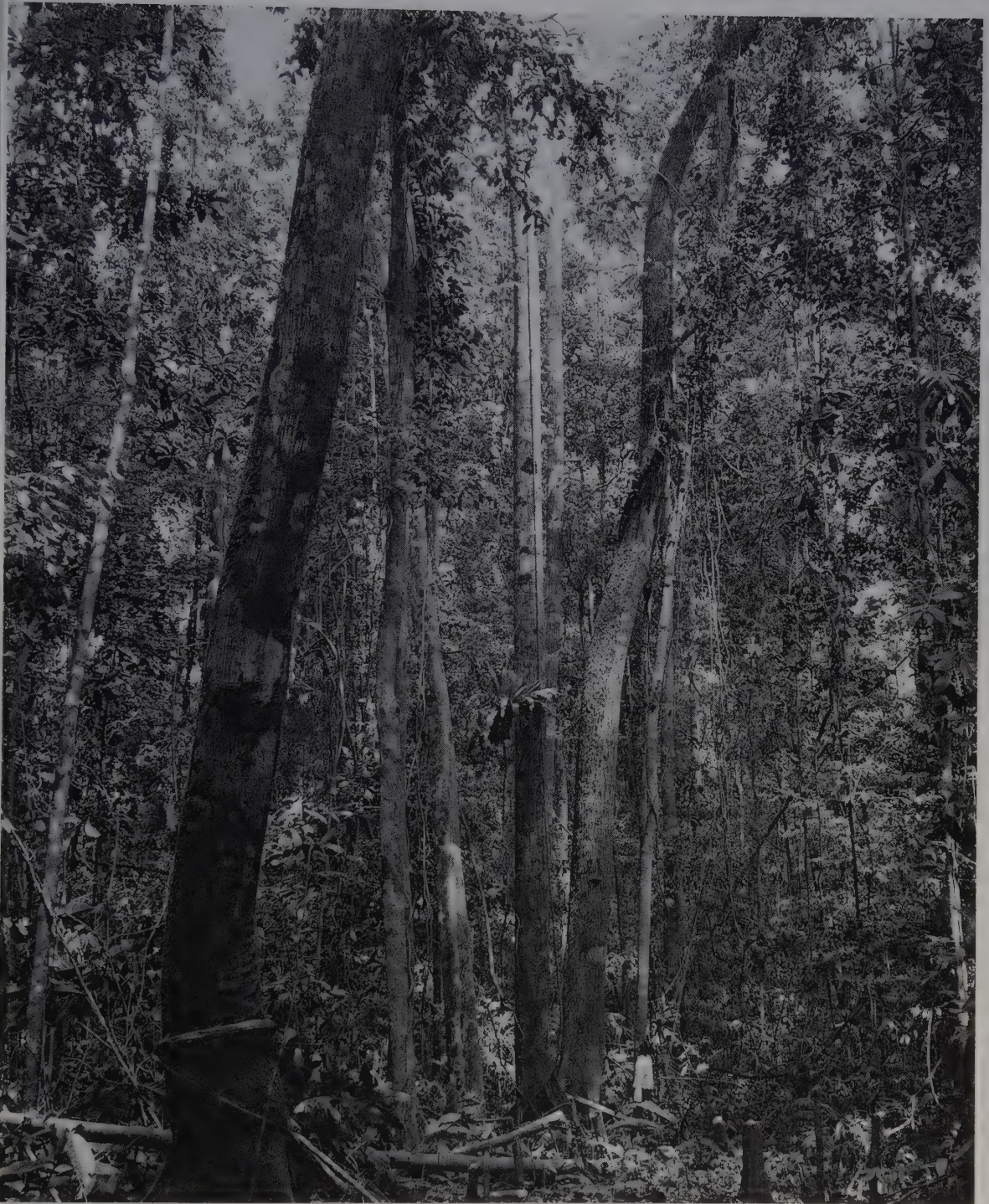
**Fig. 7.20.** Storm forest at Kemahang, northeast Malaya, in 1968, 88 years after devastation by a freak storm in November 1880. The two central trees are *Shorea parvifolia*. Many trees have a kink believed to result from regeneration through a dense tangle of climbers.

**Fig. 7.21.** Lowland rain forest, Windsor Tableland, Queensland, 12 years after logging on a polycyclic system.

Only selected big trees were felled. The canopy is more broken than in virgin forest, and the logging road (which will be used again next felling cycle) is clearly visible.

**Fig. 7.22.** Lowland dipterocarp rain forest, in Pahang, Peninsular Malaysia, shortly after logging on the monocyclic Malayan Uniform System.

All mature commercial stems have been removed, mostly dipterocarps, and the yield would have been 20–30 $m^3ha^{-1}$. The forest matrix remains intact. Note lush regrowth along the logging track.

**Fig. 7.23.** Lowland dipterocarp rain forest in Sabah, East Malaysia, shortly after logging on the variant of the monocyclic Malayan Uniform silvicultural system used there.

The forests of this region have a very high proportion of commercial stems. Removal of these, as here, commonly yields 100 m$^3$ or more of timber per hectare, and only scattered big trees remain.

the difference will depend on how many trees are felled at each cycle in a polycyclic system. The nub of the difference is that, on the one hand, polycyclic systems retain advanced growth of half-grown trees to produce marketable trees at subsequent intermediate felling cycles within the rotation. This is done by taking good care of these 'adolescent' trees at each felling. On the other hand, monocyclic systems forego the increment already accumulated in these adolescents and rely almost entirely in seedlings to produce the next crop, which will be ready to harvest only at the full rotation age. If there does happen to be any advanced growth left from the previous forest it is a bonus, over and above the seedling growth on which monocyclic systems are based.

Under the best conditions polycyclic systems can greatly increase the timber yield over a full rotation. Their success is utterly dependent on the advanced growth and this means the forest must be adequately stocked with adolescents before felling begins, and damage to them by logging kept acceptably low. If logging damage at each felling exceeds a low minimum, regeneration will be lost and the yield will progressively fall off through a series of cycles. Control can be achieved either by marking trees for retention before felling begins, which is labour-intensive, or by felling down to a rather high diameter limit.

The often-claimed disadvantage of polycyclic systems is that the faster growing genotypes are progressively removed, because at each felling many or all of the stems that have reached a minimum prescribed girth are removed. The small stems retained may be either young and potentially fast-growing or old, stunted, and unable to respond

to release. In fact, both fast and slow growth are also determined partly by phenotype (i.e. microsite) as well as by genotype. The magnitude of the disadvantage[172] is therefore anybody's guess. It can be mitigated, as is done in Queensland, by flexibility in the rules used to determine whether a tree is felled or not. In Queensland every species has a specified diameter at which it is normally felled, but vigorous individuals are retained for a later cycle and poorly formed feeble ones are felled at smaller size.

Silvicultural treatment before felling has sometimes been practised in the past in order to reduce numbers of climbers or to boost the growth of juveniles. Post-felling silviculture to remove deformed stems or to free regrowth from competition was also widely practised until recently. At its fullest development several treatments were given over the first decade or so after felling. Post-felling treatments have been largely abandoned, because of the high cost. It was demonstrated in Sarawak that a given sum of money gave a better return in terms of growth increment if invested in reducing damage by the logging operation itself rather than in post-felling silviculture. Nowadays it is generally the case that the felling operation provides the only canopy manipulation the foresters can afford.

### Criteria for success

Silviculture (Figs. 7.21–7.23) will be successful so long as it is practised within the biological limits of the forest. The desired species must be capable of growing in the size of gap that is created.

Forests are a potentially renewable source of timber, and their use for timber production is not simply a quarrying operation. The success of silviculture may be defined as the bringing to maturity of a stand of timber trees with regeneration below them to form the next silvicultural cycle, and without site deterioration such as soil erosion or degradation.

The failure of silviculture follows from working beyond the limits of the inherent dynamic capabilities of the forest ecosystem. This is commonly because rules drawn up by silviculturists are not enforced, often because of political intervention. It may also be because economists, eager to enrich a nation, apply their dismal pseudoscience to override basic biological principles and dictate the removal of a larger harvest than the forest can sustain without degradation.[173] Fuller discussion is deferred until Chapter 10.

*Woody climbers.* Unwanted 'weed' tree species can be a problem. So too can woody climbers. The natural behaviour of many of the latter is to grow vigorously in strong illumination. Thus they are common at forest fringes, such as river banks (and give rise to the myth of the impenetrable jungle), and in big canopy gaps. In many tropical rain forests the removal by logging of many trees per hectare creates large openings ideal for vigorous climber growth. In many Eastern rain forests dense carpets of the big-leaved wiry convolvulaceous climbers *Merremia* spp. smother the residual forest and form climber towers up remaining isolated trees. Trees eventually grow up and carry the carpet skywards but forest recovery is delayed and the trees may develop kinked stems (Fig. 7.20). Very little is known about the ecology of woody climbers. For example, in the Solomon Islands climbers do not proliferate excessively after cyclones but become extremely abundant after logging which causes similar canopy damage. In Sabah *Merremia*, *Mezoneuron*, and *Uncaria*, which are very serious impediments to forest regeneration, are uncommon in virgin forest, perhaps because in this country massive canopy opening does not occur naturally.

*Damage.* The amount of damage to the forest depends more on how many trees are felled than on timber volume extracted. It is commonly the case that for every tree removed for timber (logged) a second tree is totally smashed and a third tree receives damage from which it will recover (Fig. 7.24). In Queensland (Fig. 7.25) the number of stems smashed is a similar proportion but before strict rules were introduced in 1982 the proportion damaged was much higher.

The pattern of damage differs between extraction by tractor and by overhead cable, so-called high-lead logging. The latter causes extreme devastation along the paths of the cables and little between. Seedlings survive better than bigger plants. In tractor logging the damage is spread
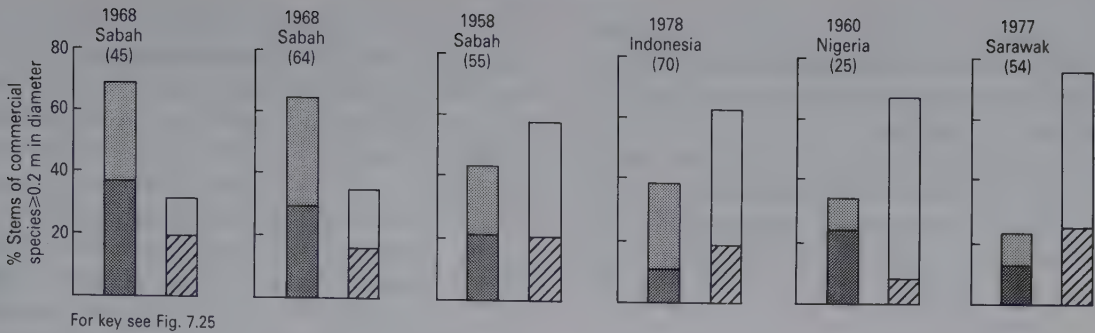
**Fig. 7.24.** Effects of logging (total commercial stems ha⁻¹ in parentheses) in various forests. (After Nicholson and Keys *ined.*)

As the number of stems lost per hectare (by logging or smashed during logging) decreases the number that survive (intact or damaged) increases. Note that in the first three forests as many trees were smashed as were logged and that the Nigerian site, which had fewest commercial stems, had fewest smashed or damaged trees.



**Fig. 7.25.** Effects of selective logging, Queensland on (a) commercial species and (b) all species, before and after introduction of strict silvicultural rules in 1982. Total stems ha⁻¹ in parentheses. (From Nicholson and Keys *ined.*)

The new rules reduced the numbers of stems smashed or damaged. Their effect was about the same on the whole forest as on just the commercial species.

more uniformly and seedling numbers can be very seriously depleted.

For successful recovery from logging the single most important criterion is to minimize damage to the forest floor, for several reasons. On the floor occur the seedlings of climax species. Within the surface soil lies the seed bank. Most of the roots and mineral nutrients are in the top 0.1–0.3 m of the soil. The surface root and humus layers allow good infiltration of rainfall. It has been clearly demonstrated several times that damage to the canopy and forest floor can be minimized by the careful planning of extraction roads and tractor paths (so-called snig tracks). In Sarawak such planning enabled 36 per cent more timber to be

moved per hour, overall costs were 19 per cent down, and open spaces in the forest were reduced from 40 to 17 per cent, with 60 commercial stems per hectare surviving rather than 40. In Queensland the new strict rules of 1982 (see above) not only reduced the numbers of trees smashed or damaged (hence increasing the number that survived intact; Fig. 7.25) but also reduced snig tracks to 9 per cent of the area, only 2 per cent with subsoil exposed.

Soil compaction along tracks is an ecological problem. Infiltration of rainfall is strongly reduced. Plants are unable to establish on these surfaces which they do not encounter naturally. Tracks can be raked to break up the compacted

soil, or specially designed tyres used on wheeled vehicles which have a low load per unit area.

Another problem created by logging is erosion, which can be disastrous (Fig. 7.26). It can be minimized by appropriate alignment and design of extraction tracks including the construction of cross-drains.[174] It is also important not to block streams or the forest is killed in the lakes that then develop.

### Silviculture in practice[175]

*Eastern tropics.* The dipterocarp forests of western Malesia are a silviculturist's dream. This is because Dipterocarpaceae of that region have the unique property amongst rain forest trees of periodic mass fruiting (p. 55) which leads to dense seedling carpets. In addition there is an unusually high proportion of the species with valuable, readily marketed timber. Amongst the dipterocarps there are both heavy hardwoods, produced by slow-growing species with very shade-tolerant seedlings, and numerous light hardwoods, produced by faster-growing species with more light-demanding seedlings. Although the forests are extremely species-rich (Fig. 2.27) with up to twenty different dipterocarps growing together in any one place, their timbers are sufficiently similar to be grouped for sale into only a handful of classes (Table 10.9). This gives a continuous supply to the consumer and ensures a steady demand.

Silviculture of dipterocarp forests developed earliest in Malaya and has shown an interesting historical development, driven by market forces. The early demand was for firewood, poles, and for naturally durable constructional timber, the 'heavy hardwoods'. This favoured management on a polycyclic system with very few stems removed at a felling; the forests were manipulated to yield these products and at the same time to release from competition small specimens of the desired species. All the more accessible forests were systematically worked for heavy hardwoods, especially *Neobalanocarpus heimii*, *Shorea laevis*, and *S. maxwelliana*, vast quantities of these being required for building construction and railway sleepers, before pressure impregnation made timber of other species durable when in contact with the ground. These heavy hardwoods were felled by axe and converted by hand-sawing into squares, baulks, and sleepers, which were then manhandled or extracted by buffalo (Fig. 7.27, 7.28).

Reconstruction after the Second World War, followed since by rapid national development and the increase in international trade, gave a big boost to demand. To start with, for the supply of sawmills, light hardwoods (*Shorea*, *Dipterocarpus*, and *Dryobalanops aromatica*) were also felled by axe and either hand-sawn into halves and extracted by buffalo or extracted as whole logs by hand-hauling on wooden sledgeways. These methods were still practised until the late 1950s.

Since then the situation has completely altered. Trees are now felled by chain-saw and extracted by winch lorry or tractor. Hard, heavy, naturally



**Fig. 7.26.** Erosion along tracks built in rain forest climates can be spectacular, as here in Malaya.



**Fig. 7.27.** Logs are still manhandled out of the peat swamp forests of Borneo.

durable timbers are less in demand than medium and light hardwoods, many of which can be impregnated with chemical preservatives if durability is required. An increasingly long list of species could be utilized as world-wide demand increased and prices rose. The necessity to get an adequate return on the substantial capital invested in vehicles, roads, sawmills, and plywood mills, made it desirable to extract all marketable species in a single felling cycle. The consequence was to change to a monocyclic system, the Malayan Uniform.[176] The extensive canopy damage, which a uniform system causes, favours regrowth of light-demanding dipterocarp species, whose rapid growth and pale, light timber makes them the desirable species to cultivate. They take *c*. 70 years to attain timber size. The first managed rotation under such a system will almost certainly contain a higher fraction of these economically desirable species than the original primary rain forest. Moreover, in a well-managed forest under a uniform system, the basal area per hectare will be lower than in only mildly disturbed virgin forest; crowns of the crop trees will have greater exposure to light and space to develop better form. All these factors favour high growth rates.

One reason for the success of the Malayan Uniform silvicultural system, where it was applied correctly, is a consequence of the unique fruiting pattern of western Malesian Dipterocarpaceae, discussed above, and which is not shown by any other major group of big rain forest trees. It will be recalled that dipterocarps fruit gregariously once every several years. Dense carpets of seedlings then develop on the forest floor which subsequently die away (Fig. 7.14), sometimes to zero, before the next gregarious fruitfall. Good regeneration is dependent on felling the forest when there are abundant seedlings. If an area is logged at a time in the cycle when seedlings are sparse disaster may result. The foresters' rule of thumb in Malaya was 'felling must follow seeding'.



**Fig. 7.28.** Elephants are used for extraction in the Malaysia-Thailand border region. Most rain forest logs are too big for them.

By the mid 1970s the Malayan forests which had seemed limitless came within sight of exhaustion. Economic pressures led to the replacement of the Malayan Uniform System, in forests well stocked with adolescent trees, by a polycyclic system. Because only large trees are removed at each cutting cycle it is possible to return for another cut every 20 or 30 years. The political attraction was that the sustainable annual coupe becomes 1/20 or 1/30 instead of 1/70 of the total forest estate.

Modified Malayan Uniform Systems were introduced into the dipterocarp forests of Sabah and Sarawak.[177] The Philippines and Indonesia both introduced polycyclic systems with the amount removed controlled by tree diameter, but this cutting limit is difficult to enforce as are the rules on road construction, so unnecessarily heavy damage commonly occurs.

The Eastern rain forests beyond the dipterocarp forest zone, east of Wallace's Line, are almost as ecologically robust because they contain numerous light-demanding species which regenerate well after heavy logging damage. Papua New Guinea suffers many natural cataclysms (see p. 116) and the islands of Melanesia are subject to cyclones. Logging merely adds a new sort of catastrophe.

The rain forest finger that extends southwards into Queensland is also subject to cyclones and most, if not all, tree species in these subtropical rain forests regenerate vigorously after logging. A polycyclic system with selective felling on a roughly 40-year cycle is practised. There is very strict control of roads and snig tracks as well as of which trees are felled and in what direction. Current silvicultural practice in Queensland provides a model showing what can be achieved, which other rain forested nations would do well to emulate (Fig. 7.21).

*Neotropics.* Silviculture of the New World rain forests is still in its infancy.[178] Research in Surinam[179] and at several places in Amazonian Brazil has found the forests to be dominated by slow-growing very shade-tolerant species with heavy timber. There is a paucity of more light-demanding species with low density timber. The heavy hardwoods respond too slowly to canopy opening to be attractive for silviculture. When the canopy is opened more than very slightly there are few seedlings able to respond by vigorous growth. In Surinam this degree of canopy disturbance leads to the forest 'tumbling down' to a mass of woody climbers and the commercially useless pioneers *Cecropia* spp. Great silvicultural skill is required to open the canopy just enough to favour *Ocotea*, the timber species with fastest growth, but not to cause this degradation.

*West Africa.* The composition of these forests seem intermediate between those of Asia and America. The ecological equivalents of the light



**Fig. 7.29.** Logs of *Tieghemella heckelii* for sliced veneer, felled under a highly selective polycyclic silvicultural system. Kumasi, Ghana. The author stands by.

hardwood dipterocarps are certain Meliaceae (the West African mahogonies), *Entandrophragma* and *Khaya*. Shade-tolerant, slow-growing, heavy hardwoods include other Meliaceae, *Guarea* and *Lovoa*, and also (as in America) numerous caesalpinoid Leguminosae (e.g. *Anthonotha, Berlinia, Cynometra, Gilbertiodendron*).

In both Ghana and Nigeria polycyclic silvicultural systems were developed, known as the Tropical Shelterwood System and Modified Selection System, which involved considerable and repeated treatment before felling. Over 200 000 ha were treated in each country between 1944 and 1966 but the systems were abandoned, partly on grounds of cost, partly because of the damage caused to the forest and the influx of climbers, and also from the realization that trees which later proved to be valuable, for example *Pycnanthus angolense*, were being poisoned. Felling was controlled by prescription of area and girth limits. Ivory Coast also for a time applied a similar system.

## 7.8. Growth rates and longevity

The wood of most rain forest species does not have growth rings and where they do occur they may not be annual so tree age cannot be measured directly. It has been found that the fastest growing juvenile trees in a forest are the ones most likely to succeed, so growth rates averaged from a number of stems are misleading. Longevity was calculated for a number of species at La Selva, Costa Rica, making due allowance for this (see Fig. 7.30). However, we have very little reliable information on how long trees can live.

Height growth rate can be spectacular. *Ochroma lagopus* (balsa) often grows 5–6 m year$^{-1}$ (Fig. 7.8). *Paraserianthes falcataria* holds the world record, 9.91 m year$^{-1}$ for the fastest individual in a Sabah plantation and 9.14 m year$^{-1}$ mean value for all 199 trees, measured at age 1.8 years.[180] Bamboo culms may grow at 1 m day$^{-1}$ for a few days by expansion of the internodes of previously formed shoots.

The forester is more interested in biomass increment. Natural lowland rain forest commonly adds 2–3 tonne year$^{-1}$ of dry weight of bole timber, which may increase to 3.6–12 tonne year$^{-1}$ in forest under good silvicultural management. Growth varies with the phase of the forest growth cycle (Fig. 7.31), from which it follows that care must be taken in obtaining or interpreting biomass increment figures from natural forests. The



**Fig. 7.30.** Estimated lifespan and growth rate of the 46 common tree species at La Selva, Costa Rica. (Data of Lieberman *et al.* 1985.) ×, Climax species with slow maximum growth rate, none reach the canopy top. ○, Climax species with medium to fast growth rate. Growth is stimulated by a canopy gap. Most reach the canopy top. ●, Pioneer species. Growth rate is fast to very fast. All except the slowest-growing reach the canopy top.



**Fig. 7.31.** Growth of a freely growing tree and its relation to the forest growth cycle. (Whitmore 1984*a*, Fig. 9.3.)

forester aims to harvest trees in both natural forest and plantations at about the time they mature and growth slows down. In plantations tropical conifers grow faster than broadleaf species (Fig. 7.32).

## 7.9. Forest recovery after human disturbance

The time climax rain forest takes to return to a site depends on the severity of the disturbance.

Low intensity selective logging on a polycyclic system closely mimics the natural processes of forest dynamics and scarcely alters the composition. Monocyclic silvicultural systems and polycyclic systems with many stems felled per hectare shift species composition to increase the proportion of the more light-demanding, faster-growing tree species. Areas that are laid bare by timber extraction develop a secondary forest of pioneers. Compacted soil will be only slowly colonized by trees but will usually soon be covered by creeping plants or thicket-forming resam ferns (*Gleichenia* s.l.). Where streams have been dammed by tracks without culverts swamps develop and the forest is killed. Thus a logged forest becomes a very complex mosaic of vegetation types, including true secondary forest, relict patches of primary forest, and depleted forest from which some species have been removed for timber. Repeated logging increases depletion and eventually all or most of the big trees may be lost. A dense, low, climber-tangled forest develops. Such derelict forests are common near to towns where timber theft is a serious problem. In some ways they can be viewed as green deserts.

If land is clear-felled and then abandoned it is quickly reoccupied by forest. The composition differs if the cleared site is burned. Regrowth is partly of pioneers germinated from seed, partly of surviving seedlings, and partly from root and stem sucker shoots. Burning may alter the composition of the pioneer flora, and will reduce the amounts of vegetative sprouts and surviving seedlings.

If land cleared and used for pasture or for growing crops is abandoned forest will soon develop. The pioneer woody species may differ from those that colonize land that has not been farmed. For example *Melastoma* becomes common in the Eastern tropics. This is partly because the soil has lost nutrients and becomes more acid and compacted (section 8.1). In addition during the cultivation period the soil seed bank becomes progressively depleted as does the capacity of roots and trunks to develop coppice shoots. Regrowth in these circumstances is from seed rain. Pioneers soon arrive, but the rapidity of later succession is strongly dependent on there being climax species nearby. In Mexico it was shown that climax species reinvaded around relict trees left on the farmers' fields because these provide bird perches.[181] A few years after the fields were abandoned the area became covered by secondary forest of pioneers within which were nuclei of climax species. At Kepong, Malaya, the first dipterocarp colonized in 1976 a field abandoned in 1944. The nearest parent tree was only 180 m distant.[182]

Starting in the early 1970s huge pastures covering thousands of square kilometres have been created out of rain forest in Pará State, southeast Amazonia. Cattle raising proves unprofitable and many holdings are abandoned after a few years. Woody vegetation soon returns, but the prognosis for the spontaneous restoration of climax forest is gloomy, because of the absence of seed trees.
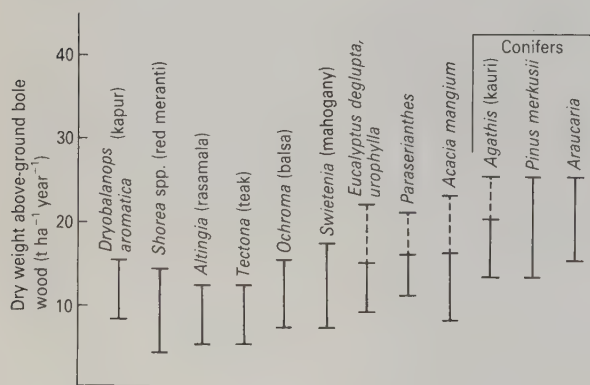


**Fig. 7.32.** Timber yield of various species grown in plantations. (Whitmore 1984*a*, Fig. 9.1 updated.)

**Fig. 7.33.** The tree fern *Cyathea contaminans* colonizing bare ground at the margin of lower montane rain forest, Cibodas, west Java.

## 7.10. The dynamics of climax rain forest

The forest canopy is in a continual state of flux as this chapter has sought to demonstrate. Scientists have wondered whether composition changes with time or fluctuates about a mean. This is, in fact, a question impossible to answer with any degree of certainty because of the long time-scale involved. Trees certainly commonly live for a century or more, even though precise ages are hard to determine, and no permanent sample plots are older than a few decades. An individual tree only needs on average to have a single successful seedling for floristic composition to be maintained. This gives time for a great deal of short-term fluctuation in seedling recruitment and mortality.

In Ghana there is a broad cline in species composition from southwest to northeast over a distance of 300 km, which is probably determined by a combination of soil type and the increasingly seasonal and dry climate.[183] Forests at different places along this cline seem to 'breed true', juvenile populations being most similar to the ajdacent adult populations. At any one place there are big differences between species in their population dynamics. The numbers of juveniles give no indication of recruitment of adults. The two extremes are represented by *Celtis mildbraedii* and *Strombosia glaucescens*.[184] Most *Celtis* are over 0.3 m in diameter, smaller plants are very rare but extremely persistent. *Strombosia*, by contrast, has very few trees over 0.3 m in diameter and numerous smaller plants which have a rapid turnover. Both species seem to be maintaining themselves but by differing means. Similar differences were found amongst seedlings on Kolombangara Island in the Solomons where in most years *Calophyllum kajewskii* and *C.vitiense* recruit often extensive

populations of 300–2400 seedlings ha⁻¹ of which up to three-quarters die within a year. In the same forest *Dillenia salomonensis* and *Parinari salomenensis* have populations of only 30–170 seedlings ha⁻¹ with rare recruitment and little mortality.[185]

In the Okomu forest, Nigeria, E. W. Jones found that the largest trees, including strongly light-demanding *Entandrophragma* spp. were scarcely regenerating.[186] On further investigation it was found the area had once been agricultural land but had been abandoned during tribal wars at least 200 years previously. The regrowth forest came to be dominated by light-demanding species, and by the time of Jones' study these were being replaced by more shade-tolerant ones in the absence of further massive disturbance. The publication of these discoveries caused something of a sensation, because this was the first strong evidence that tropical rain forests are not necessarily ancient and immutable.

Permanent sample plots are essential for the monitoring of change of composition with time. At Sungei Menyala, Malaya, a 2 ha plot has been under observation since 1947.[187] Here the topmost trees are mostly light hardwood dipterocarps, climax species with fairly light-demanding seedlings. The middle-sized trees contain more heavy hardwood dipterocarps, species with more shade-tolerant seedlings. The whole plot originally contained 1075 trees over 0.1 m in diameter. During the 38 years of observation 697 of these had died (64.8 per cent) which is a considerable turnover. Substantial canopy damage was noted after windstorms in 1948 and 1958 and during the 1970s. The overall effect at Sungei Menyala has been for the amount of disturbance experienced to maintain the same proportion of the two ecological species classes (light and heavy hardwoods) in the different parts of the canopy.

Another long-term investigation has monitored 22 plots of total area of 13.7 ha over periods up to 21.3 years on Kolombangara Island. Big differences were found between periods and from place to place (Figs. 2.22, 2.23) in the amount of canopy disturbance, with a maximum 67 per cent and a minimum 0.6 per cent (Fig. 7.34a). This study[188] shows that either small sample plots or short study periods look at the flux in a forest canopy through only a tiny 'window' and may give extremely misleading results, not applicable to the whole forest. It is commonly stated that trees die or that canopy gaps form at an annual rate of about 1–2 per cent, but the Kolombangara observations show that this average figure might conceal more than it reveals.
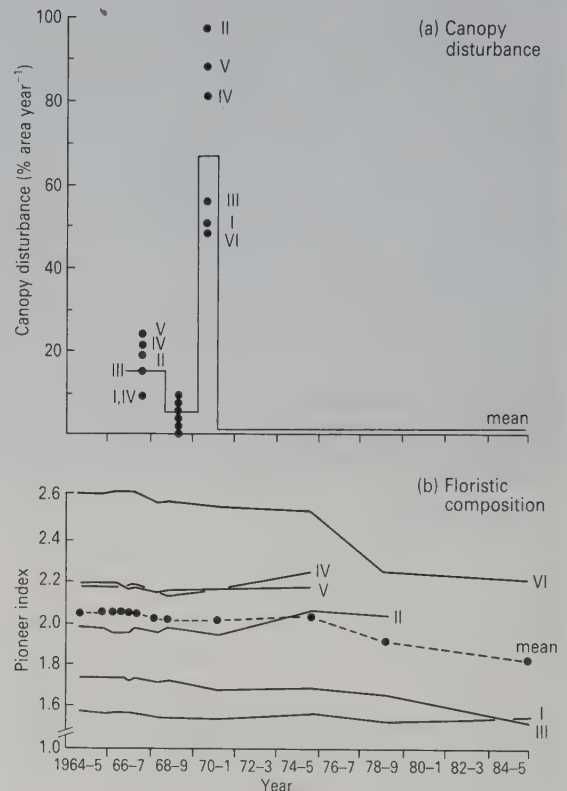


**Fig. 7.34.** Forest dynamics of the lowland rain forests on Kolombangara, Solomon Islands, 1964–1986. Six forest communities (I–VI) of different floristic composition. (a) Canopy disturbance during different time periods. (b) Floristic composition through time. (Whitmore 1989b, Figs. 2,5.)

(a) shows that canopy disturbance varied from time to time and different forest floristic types suffered different disturbance. On (b) floristic composition is expressed as a pioneer index which reflects the proportion of light-demanding, big tree species. The mean pioneer index dropped with time but with substantial differences between the six forest types, two of which actually showed a slight increase. Overall the amount of disturbance was insufficient to maintain the proportion of light-demanders present at the start of the study.

The Kolombangara survey also threw light on the question posed above of stability of floristic composition through time. Differences that existed in species composition between the sample plots at the outset of the survey were believed to be principally due to spatial variation in amount of past canopy disturbance, with consequent differ-ences from place to place in what species had been recruited in gaps. During the 21.3 years of obser-vation the floristics progressively changed (Fig. 7.34b), because the amount of canopy disturbance was insufficient to maintain this initial composi-tion.

## 7.11. Forest dynamics—Chapter summary

1. The study of forest dynamics is currently very active and findings in tropical rain forests have close parallels in other types of forest.

2. There is a range of different forest micro-climates. In particular, light varies in spectral composition and in quantity both in time and in space.

3. There are two classes of tree species, pioneer and climax. The essential differences are that pioneer species germinate only in full light in a canopy gap after its creation, so their seedlings are not found below a canopy. Climax species by con-trast usually germinate below a canopy and their seedlings are shade-tolerant. Each species class is characterized by a whole syndrome of ancillary features (Table 7.4) which are adaptive to the eco-logical niche it occupies. The two classes are sometimes called light-demanders and shade-tolerants, by reference to their seedling ecology.

4. Within each class there are species with dif-ferent characteristics but variation is continuous. Pioneers can usefully be divided by usual height attained at maturity (Table 7.3) and climax species by the degree of seedling shade-tolerance (Table 7.5). The most light-demanding climax species re-semble pioneers except for their ability to germin-ate below a canopy.

5. Pioneer species colonize big canopy gaps. Be-low them climax species establish. As the pioneers die, creating small gaps, the climax species grow up to succeed them.

6. All rain forest soils investigated contain a seed bank, mostly composed of pioneer species. Pioneer species have orthodox seeds, capable of dormancy.

7. Tropical pioneer tree species have been shown to have seed germination triggered either by light in which the red wavelengths exceed the far-red (Fig. 7.13), or by elevated temperature. Both conditions are found in gaps but not below a closed canopy (Fig. 7.2, Table 7.2).

8. Many climax species have recalcitrant seeds which cannot be stored and which germinate im-mediately. They form seedling banks on the forest floor and await a canopy gap to start upward growth.

9. Species differ in the microsite conditions in which their seedlings establish most successfully. The coexistence of numerous species in tropical rain forest depends on many facets of their re-generation, including microsite specialization.

10. A forest is most species rich when at an in-termediate state of recovery from disturbance, or when disturbance is at an intermediate intensity or frequency, because it then contains both pioneer and climax species.

11. Light-demanding species have higher unit leaf rate than shade tolerants (Table 7.7). Seedling shade-tolerance includes the ability to utilize intermittent sunflecks and in having a low res-piration rate relative to photosynthesis (Table 7.8).

12. Regions of the tropics differ in the frequency of catastrophic disturbance and hence in the abundance of light demanders in their forests. Ex-tensive fires have occurred in rain forests recently in Asia and in the past in South America.

13. Silviculture, the manipulation of the forest canopy to favour certain species, exploits the dif-ferent gap requirements for regeneration, i.e. dif-ferences in shade tolerance. Polycyclic systems repeatedly remove trees as they mature leaving all

adolescent trees to swell future yields. Monocyclic systems remove all marketable trees at a single operation (so create bigger canopy gaps) and rely on seedlings for the new crop. Polycyclic systems thus tend to favour shade-tolerants and mono-cyclic systems to favour light-demanding species. With good control over damage polycyclic systems yield more timber.

14. The ecology of most rain forests is sufficiently well-known for viable silvicultural systems to be devised, whereby the forest can be maintained as a continual source of timber. You can both 'have your cake and eat it' provided sufficient care is taken to work within the biological limits of the forest. Where silviculture fails it is usually because the rules are not enforced. Diptero-carp rain forests have easy silviculture because they contain numerous light-demanding commercial species which grow fast after canopy opening.

15. Big woody climbers are always a problem to silviculture, and sometimes small weedy pioneer trees too, because they are strongly stimulated by canopy opening.

16. Nowadays the canopy opening caused by timber extraction is usually the only silvicultural operation that can be afforded; formerly pre- or post-felling treatments were applied.

17. The greater the disturbance of a climax forest the longer it will take to recover. Climax species are slow to recolonize land that has been totally cleared unless seed trees remain.

18. Growth rates are difficult to estimate be-cause rain forest trees lack annual rings. The fast-est growing juveniles are most likely to reach maturity. Biomass increment can be increased by silvicultural treatment but is less in natural forest than in plantations. Height growth rates of some pioneers are spectacular.

19. The rain forest canopy is in a state of con-tinual flux and different tree species have different recruitment and death rates. It is difficult to know whether a climax forest maintains the same species composition over several forest growth cycles be-cause sample plots are too small or too shortlived to sample more than a tiny part of the spatial and temporal flux.

# 8

# Nutrients and their cycles

This chapter investigates the effects of Man's usage of tropical rain forests on the ecosystem's capital stock of plant mineral nutrients and on their cycles. First the nutrient cycling aspects of shifting agriculture are described, then nutrients and their cycles in primary rain forest. Based on this we discuss the effect on nutrients of different intensities of forest exploitation and the limits of sustainable utilization. The chapter concludes with discussions of the role nutrients might play in determining the distinctive structure and physiognomy of the heath forest and upper montane rain forest formations.

## 8.1. Shifting agriculture

The trees and other vegetation are felled to lie uniformly; they form a fuel bed which is allowed to dry for six or more weeks ... The fields are burned a few weeks before the end of the dry season ... Fuel breaks are prepared ... to prevent the escape of fire ... At about midday when conditions are hottest and driest [torch bearers] begin to light the fuel bed starting on the ridges. As the fuel burns it causes an indraft, and by the time the fire reaches the lower edges of the fields a strong wind is blowing into the fire ... of 40 to 65 km per hour. Small intense firestorm whirlwinds ... spiral masses of flame up to 100 m tall, developing intense winds at their centres.[189]

Fire is an essential tool of the peasant rain forest farmer (Fig. 8.1). The essence of shifting agriculture (sometimes called swidden agriculture) is to fell a patch of forest, allow it to dry to the point where it will burn well, and then to set it on fire. The plant mineral nutrients are thereby mobilized and become available to plants in the ash. One or two fast maturing crops of staple food species are grown (Fig. 8.2). Yields then fall and the patch is abandoned to allow secondary forest to grow. Longer-lived species, such as chilli (*Capsicum annuum*) and fruit trees, and some root crops such as cassava (*Manihot esculenta*) are planted with the staples and continue to yield in the first years of the fallow period. Besides fruits and root crops the bush fallow, as it is often called, provides fire-wood, medicines, and building materials. After a minimum of 7 to 10 years the cycle is repeated.

There are many variants. Shifting agriculture was invented independently in all parts of the



**Fig. 8.1.** Shifting agriculture in Sarawak. Iban farmers watch as fire. burns the felled and dry bush fallow on next season's field.

tropical world[190] and has proved sustainable over many centuries. In Asia dry land cultivars of rice are the staple crop, in New Guinea and Melanesia sweet potatoes or taro (*Ipomoea batatas; Alocasia macrorrhiza, Colocasia esculenta*) are grown, in Africa and in the New World maize, beans, and squash (*Zea mays, Phaseolus* spp., *Cucurbita* spp.) are commonly planted in mixture. For the later years, in Nigeria it is common to plant oil palm and the two fruit trees *Irvingia gabonensis* and *Pentaclethra macrocyla* (African oil bean)[191] and in southeast Asia bananas (*Musa*) are important.

Crop yields diminish because the soil becomes exhausted (as discussed below) and also because of a build-up of pests, diseases, and weeds. In Sarawak the most pernicious weeds are grasses (including alang alang, cogon or lallang, *Imperata cylindrica*) and sedges, mainly *Cyperus* and *Scleria*, because they spread rapidly from seeds and also from even tiny fragments of rhizome if these are overlooked when the crop is weeded.[192]

The forest regrows partly from coppice shoots and partly from seeds. Farmers have learned that certain species indicate that regrowth will be vigorous, and that if cultivation is continued for too long other species colonize which grow less strongly, or rhizomatous weeds such as *Imperata* get too strong a hold to be eliminated by the fallow. Farmers therefore know when the field should be abandoned to allow successful regrowth, with the possibility to return for another cycle of cultivation in a few years' time. It is easier to fell and burn secondary forest than virgin jungle and repeated rotation through an area is often preferred to continual movement into new areas.

It is now realized that shifting agriculture, as traditionally practised, is a sustainable low-input form of cultivation which can continue indefinitely on the infertile soils underlying most tropical rain forest (Table 8.1), provided the carrying capacity of the land is not exceeded. Moreover, many shifting cultivators have great skill and sophistication.[193] The old idea of colonial days that it was a wholly bad practice has been repeatedly refuted, but still dies hard amongst some contemporary politicians. Shifting agriculture involves the rotation of fields rather than crops, and by this means breaks the build-up of pests, diseases, and weeds in a con-

tinuously wet climate where there is no cold or markedly dry season.

Shifting agriculture has the limitation that it can usually only support 10–20 persons $km^{-2}$, though occasionally more (Table 10.1) because at any one time only *c*. 10 per cent of the area is under cultivation. It breaks down if either the bush fallow period is excessively shortened or if the period of cultivation is extended for too long, either of which is likely to occur if population increases and a land shortage develops.

There is, however, another mode of shifting agriculture which is totally destructive (Fig. 8.3). Farmers fell and burn the forest and grow crops on the released nutrients for several years in succession, continuing till coppicing potential and the soil seed bank are exhausted, pernicious weeds invade, and soil nutrients are seriously depleted.

Table 8.1

*Soils of the humid tropics and their extent grouped by main features*

|  | Percentage of area |
|---|---|
| Old infertile loamy and clayey soils (oxisols and ultisols) | 63 |
| Relatively more fertile, less weathered soils: of locally less leached conditions (alfisols and vertisols) | 4 |
| on mainly alluvial lowlands (fluvents and aquepts) | 12 |
| on volcanic ash (andosols) | 1 |
| on steep slopes (tropepts and lithic soils) | 11 |
| Infertile sands (spodosols and psamments) | 7 |
| Infertile peats (histosols) | 2 |

Based on Sanchez (1976); Vitousek and Sanford (1986). For further information consult Burnham in Whitmore (1984*a*)

The major categories within each group are given, using the terminology of the United States Department of Agriculture Soil Classification: 7th Approximation. It is shown that, although over half the tropics have infertile soils, only a small percentage are extremely infertile and, contrary to popular perception, there are also big areas of relatively fertile soils.

**Fig. 8.2.** Shifting agriculture in Venezuela. A small clearing made by Amerindian farmers, the crops beginning to grow.

They then move on to a new patch of virgin forest. This is happening, for example, in parts of western Amazonia, practised by peasants from the high Andean plateau who have moved down the eastern slope of the Andes, along new government-sponsored roads to escape overcrowding, and have no prior experience of forest-farming. In these countries the act of forest clearance gives title to the land. After growing a few crops they sell-out to a pastoralist who attempts to grow cattle. Thus there is a moving front of cultivation with poor pasture behind invading Amazonia from its western foothills. In mainland southeast Asia the Hmong people have practised migratory destructive shifting agriculture for centuries.[194]

**How shifting agriculture works**

The above-ground biomass of a forest contains plant mineral nutrients and these are mobilized when it is burned. Nitrogen and sulphur are volatilized in smoke, but the other nutrients remain in the ash and are available to plants. There is a reduction of about one-quarter in soil organic matter. Herbaceous crops have shallow roots and take up nutrients from the surface layers. Yields drop as nutrients are either taken up, leached, lost by surface erosion, or become unavailable.[194a] The soil becomes more acid as nutrient cations are depleted and aluminium may become soluble as

$Al^{3+}$. This ion is toxic to plants, and crop plants are especially sensitive. The important nutrient phosphorus quickly combines with aluminium as insoluble compounds and becomes unavailable to the crop plants, for which it is often critically deficient.

The native woody species of the bush fallow are less sensitive than crops to acid soils and to soluble aluminium. They also have deeper roots than herbaceous crops. It is likely that some are able to unlock phosphorus and utilize it, perhaps using the mycorrhiza with which their roots are infected. Thus the regrowth forest is able to thrive even though crops cannot. Nutrients are progressively restored to the above-ground biomass as the regrowth forest develops, as shown in Fig. 8.4. Soil organic matter builds up and improves the soil structure. Secondary forest continues to increase in biomass for many decades, but nutrients accumulate most rapidly over the first decade or so and by 8–10 years of age may approach their former levels. This is because the concentration of mineral nutrients in the parts of a tree is leaves > twigs > branches > trunks, and most of the leaves and twigs are restored in the first few years. Later on the main growth is as the addition of boles and branches.

Some farmers improve the efficiency of the bush fallow. In northeast India the alder tree *Alnus nepalensis* is planted.[195] This has the added

**Fig. 8.3.** (a) Sustainable (cyclic) and (b) unsustainable (invasory) shifting agriculture. (Rijksen 1978, Fig. 146.)
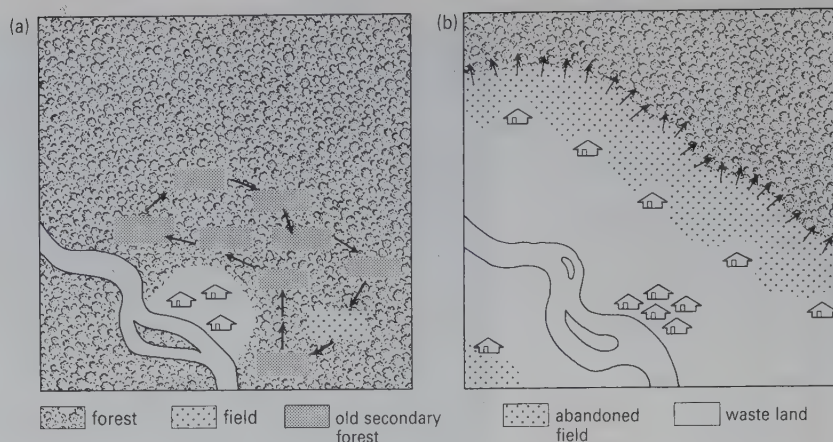


**Fig. 8.4.** Restoration of nutrients and biomass in forest regrowing after felling and burning. Tropical semi-evergreen rain forest, Colombia. (Data of Fölster *et al.* 1976; Jaffré 1985 gives further examples.)
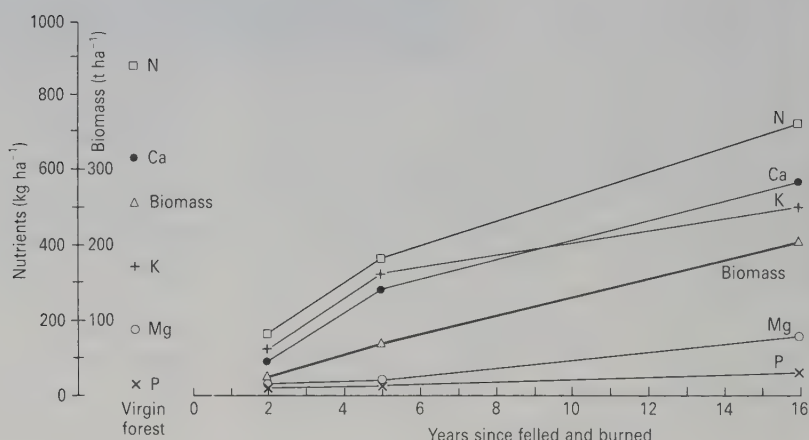
bonus of strongly coppicing, so quickly regrows in the fallow. In the highlands of New Guinea *Casuarina oligodon* is planted for use as firewood. Both *Alnus* and *Casuarina* fix atmospheric nitrogen via root nodules inhabited by the fungus *Frankia*. In Nigeria *Acioa barteri*, *Anthonotha macrophylla*, and *Dialium guineense* are all planted to improve the nutrient status of the fallow. In northeast India natural fallow rapidly builds up potassium in the herbaceous climber *Mikania micrantha*. Later in the succession the same role is played by the bamboo *Dendrocalamus hamiltonianus*.

## 8.2. Nutrient pools and cycles in primary rain forest[196]

The study of plant mineral nutrients in tropical rain forest ecosystems, both above and below ground, has been slow to develop. There are practical problems in the assay of nutrients in the different compartments, leaves, twigs, wood, and bark. The above-ground biomass of primary lowland forest is usually *c.* 400 tonne ha$^{-1}$ and a sophisticated system of subsampling must be devised. A considerable fraction of the root biomass is in fine roots which are very difficult to extract (p. 51). Different standard chemical methods of assaying soil nutrients are not directly compar-
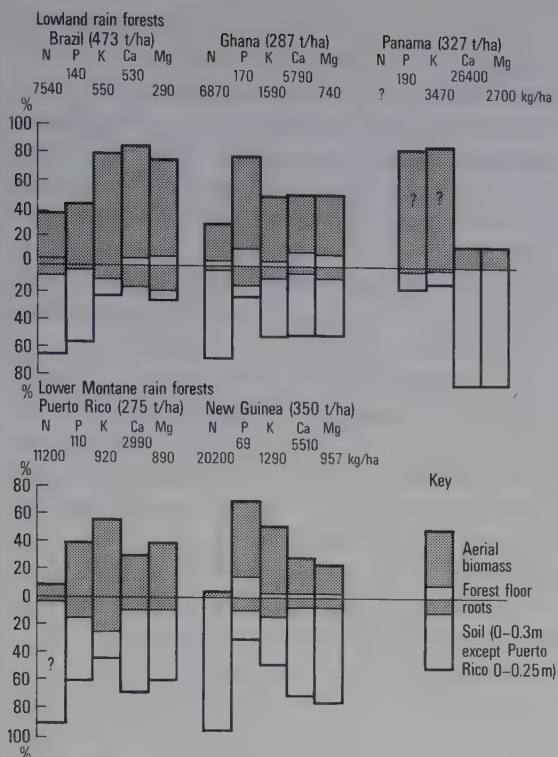
**Fig. 8.5.** Distribution of inorganic nutrients above and below ground in various tropical rain forests. Biomass in parentheses. (Whitmore 1984*a*, Fig. 10.2.)

> Note that the popular belief that most of the nutrients of a tropical rain forest are in the biomass is seldom true.



**Fig. 8.6.** Simplified diagram of inorganic nutrient cycling in a rain forest. Figures (in kg ha$^{-1}$ or kg ha$^{-1}$ year$^{-1}$) are for the lower montane rain forest at Kerigomna, New Guinea. (After Edwards 1982 in Whitmore 1984*a*, Fig. 10.1.)

able. There are now enough studies, despite these difficulties for the glimmerings of a coherent picture to be visible.

## Nutrient capital

The division of the ecosystem nutrient capital between above- and below-ground compartments is shown for three lowland and two lower montane forests in Fig. 8.5. It was until recently believed that nearly all the mineral nutrients in tropical rain forests are in the above-ground biomass. This is certainly the case for the soluble cations $K^+$, $C^{2+}$, and $Mg^{2+}$ in the Brazilian forest but not so elsewhere. The significance of the recorded levels of nitrogen and phosphorus in the soil is difficult to evaluate because much is probably in forms unavailable to the plants.

## Nutrient cycles

The main flows of nutrients are shown in Fig. 8.6, using the example of a lower montane rain forest in New Guinea. There is input from rainfall of nutrients in solution as well as by particulate aerosols. It was noted above that forest burning causes loss of nitrogen and sulphur in smoke, but what one shifting farmer loses another one nearby gains when the air is washed clean by rain. Some rain reaches the ground by trunk flow, but except after heavy storms 99 per cent of water reaching the ground penetrates the canopy as throughfall. As it does so nutrients are leached from the leaves, so the concentration in throughfall is greater than in rainfall. In the New Guinea example (Fig. 8.6), the soluble cations $K^+$ and $Mg^{2+}$ were enhanced about 9 times, $Ca^{2+}$ and phosphorus 5 times, and nitrogen 4.6 times. The enhancement of nitrogen was believed to be due to leaching from nitrogen-fixing epiphyllous algae (p. 43).

Besides nutrients in throughfall and stemflow the forest floor also receives them from litterfall.

This is conventionally divided into two compon-
ents, fine and coarse litter. Fine litter is mainly
leaves but also includes flowers, fruits, and fine
twigs. It is relatively easy to set up a system of
traps, for example fine nylon-mesh trays, and to
obtain a statistically satisfactory record of fine litter-
fall over a year or two of study. Coarse litter, which
is branches, limbs, and falling tree trunks, is very
heterogeneous in both space and time and it is
much more difficult to get a meaningful record,
although in amount coarse litter may exceed fine
litter.

After the litter has decomposed (see below) the
nutrients pass into the mineral soil and may be
taken up by the roots or leached out into streams.
There may also be nutrient input into the soil
from the breakdown of soil minerals. These may
either be part of the rock on which the soil lies or
in some places may be volcanic ash which has
been carried in after eruptions, perhaps from
many hundreds of kilometres away.

Most of the plant roots are in the top 0.1–0.3 m
of the soil (p. 51). This layer of roots is important
for the uptake of nutrients which enter the soil
surface. Its disruption, for example, by a careless
logging operation (p. 122), thus has serious con-
sequences. Most tree species have mycorrhizas
and these enhance nutrient uptake, especially
phosphorus.

All rain forests receive small amounts of nutri-
ents in rainfall. Some nitrogen is converted to
nitrates in thunderstorms. For other nutrients the
amounts received are highest near the sea and
very low a long way inland, for example in central
and upper Amazonia.[197] There is an important
distinction between rain forests on deep soils
which receive nutrients solely in rainfall and
others with soil parent material within the rooting
zone which also receive them from that material.
In the former, nutrient cycles are almost closed,
and recycling is very important. In the latter the
cycles are more open. Table 8.2 shows the much
higher concentrations of certain major nutrients
in young shallow soils in Sabah, c. 0.4 m thick,
contrasted to old deep soils in Malaya, 2–20 m
thick, where the soil parent material is the same
but is no longer within rooting depth.

Many of the world's rain forests are on rugged,
hilly terrain where the soil is shallow and con-
tinually being rejuvenated by creep and landslip.
Unless the parent material is very low in nutrients
(as are the sedimentary soils of parts of Sarawak),
these ecosystems have a continual input of nutri-
ents from decomposing rock.[198] By contrast, rain

Table 8.2
*Plant mineral nutrients within the soil*

| Parent material | Nutrient concentration (m equiv 100 g$^{-1}$) | | | | |
| | Ca | Mg | K | Na | Total |
|---|---|---|---|---|---|
| Young soils, 0.4 m thick, Sabah (sampled 0.1–0.4 m) | | | | | |
| Sandstone and shale | 0.16 | 0.09 | 0.05 | 0.06 | 0.36 |
| Limestone | 52.35 | 1.27 | 0.26 | 0.13 | 54.01 |
| Serpentine | 36.35 | 11.40 | 0.02 | 0.42 | 48.19 |
| Basalt | 5.67 | 8.53 | 0.06 | 0.42 | 14.66 |
| Old soils, 2–20 m thick, Malaya (sampled 0.8–1 m) | | | | | |
| Shale | 0.19 | 0.08 | 0.20 | 0.24 | 0.82 |
| Limestone | 0.42 | 0.11 | 0.24 | 0.22 | 0.99 |
| Serpentine | 0.30 | 0.38 | 0.33 | 0.16 | 1.21 |
| Basalt | 0.20 | 0.04 | 0.12 | 0.14 | 0.72 |

From Burnham in Proctor (1989)
The amounts of nutrients in the young, shallow soils differ between parent materials (e.g. high Ca over limestone)
and are mostly greater than in the old, deep soils where parent material has little or no influence.

forests on flatter terrain or older deeper soils have no such input. Even if there is addition of nutrients at the bottom of the soil profile, in old, deep soils it is beyond rooting depth, outside and uncoupled from the ecosystem. The most extensive very deep soils occur in central Amazonia, where the forests lie on a huge sedimentary Tertiary plain.

It has been shown that the amounts of most nutrients lost in streamwater vary with the lithology of the catchment and is especially low from the infertile soils of the central Amazon, in contrast to forests over fertile substrates, for example andesites in Papua.[199] There is also less annual nutrient loss from forests in seasonal climates. Phosphorus does not follow this pattern, because it always becomes immobilized.

Comparisons of quantities of nutrients in fine litterfall and in leaves still attached to the trees show that lowland rain forests cycle little phosphorus in their litterfall. Montane rain forests, by contrast, cycle little nitrogen. The implication is that phosphorus is a limiting nutrient in lowland ecosystems (as is well-known to tropical farmers), but that in the mountains nitrogen is more strongly limiting.[200]

### Decomposers

Litter on the forest floor must decompose before its nutrients become available for plants. There have now been many studies made on the rates of fine litter fall[201] and its decomposition. Table 8.3 gives a sample. In the lowlands decomposition

Table 8.3

*Fine litter: fall, average amount, and disappearance in various rain forests*

| Forest formation and place | (a) Fine litterfall (t ha$^{-1}$ year$^{-1}$) | (b) Forest floor (t ha$^{-1}$) | (c) Decay factor, $k$ (a)/(b) |
|---|---|---|---|
| **Lowland evergreen rain forest:** | | | |
| Mulu, Sarawak: ridge | 7.7 | 5.9 | 1.3 |
| valley alluvium | 9.4 | 5.5 | 1.7 |
| Pasoh, Malaya | 10.6 | 3.2 | 3.3 |
| Penang, Malaya | 7.5 | 4.9 | 1.5 |
| Manaus, Brazil | 7.6 | 7.2 | 1.1 |
| **Lowland semi-evergreen rain forest:** | | | |
| Barro Colorado, Panama | 13.3 | 11.2 | 1.2 |
| Kade, Ghana | 9.7 | 4.9 | 2.0 |
| **Heath forest**, Mulu, Sarawak | 8.1 | 6.1 | 1.2 |
| **Forest over limestone**, Mulu, Sarawak | 10.4 | 7.1 | 1.5 |
| **Freshwater swamp forest** Tasek Bera, Malaya | 9.2 | 4.8 | 1.9 |
| **Montane rain forests:** | | | |
| New Guinea, 4 close sites (*c.* 2500 m) | 6.2–6.6 | 4.2–6.6 | 1.0–1.5 |
| Colombia (1630 m) | 10.1 | 16.5 | 0.6 |
| Costa Rica, Volcan Barva† | | | |
| 1000 m | 6.6 | 4.2 | 1.6 |
| 2000 m | 5.8 | 5.2 | 1.1 |
| 2600 m | 5.3 | 6.3 | 0.8 |

Mainly from Whitmore (1984*a*, Table 10.8); Anderson and Swift in Sutton *et al.* (1983, Table 1)

† Heaney and Proctor (1989)

occurs in 4–12 months,[202] similar to the rates reported for other climates. The common supposition that litter disappears from the floor of tropical rain forests uniquely rapidly is not borne out by these figures. There is more variability in the amount of litter on the forest floor than in the rate of fall, which implies that differences lie mainly in the rate of decomposition. The scanty data collated in Table 8.3 suggest that decomposition is slower in montane forests (see p. 147 below).

In most soils the main decomposers are litter-feeding invertebrates. Termites are a major component of this so-called soil macrofauna,[203] but in montane forests earthworms replace them. On Gunung Mulu, Sarawak, no termites were found above 1860 m. Both termites and earthworms comminute litter as well as contributing to its decomposition. There are five families of lower termites. All have protozoan symbionts in their guts

which decompose cellulose. The single higher termite family, Termitidae, dominate many rain forest soils and have bacterial gut symbionts which perform the same role. One of its subfamilies, Macrotermitinae, is widespread in rain forests, and uses mainly fresh plant material to cultivate subterranean fungus combs or 'gardens'. The fungus breaks down both cellulose and lignin and the termites feed on the food bodies that it produces. Macrotermitinae are especially frequent in more seasonal and drier climates, because the fungus combs can digest fresh, dry food-materials not utilizable by other termite groups. In Sarawak they were shown to be commoner in logged forest. Many are serious pests, attacking food- and tree-crops as well as timber buildings. Alterations in the decomposer community which increase their abundance may have undesirable consequences.

## 8.3.  Practical implications

Mankind makes use of tropical rain forests or their soils in many ways as will be explored in Chapter 10. An important requirement for sustainable utilization without degradation is to work within the ecosystem nutrient budgets and cycles, and in the case of forest utilization not to disrupt these by excessive damage. Knowledge has developed far enough to indicate some of the major constraints.

Utilization of forests or forest soils involves removal of products and their nutrient content. The nutrient capital will run down if removals exceed inputs. Thus there may be substantial differences between forest ecosystems with closed and open nutrient cycles.

*Timber removal.*    Human impacts on rain forests vary in severity. The selective removal of the boles of one or a few trees per hectare for timber leaves most of the nutrient capital behind. This is because nutrients are most concentrated in the branches, twigs, and leaves. With increasing volume of timber removed, the amounts of nutrients removed also increase. Loss from the ecosystem is reduced if bark is left in the forest and only the wood extracted. Table 8.4 demonstrates

for a lower montane rain forest in Papua New Guinea, which was under timber exploitation, that only 12–41 per cent of major plant nutrients were in the bole wood of all trees 0.1 m in diameter and over. Their total biomass was 295 tonne ha$^{-1}$ of which only *c*. 10 per cent (30 t ha$^{-1}$) were extracted as timber, so less than 5 per cent of above-ground ecosystem nutrients were being removed. From Fig. 8.5 it can be seen that in this forest there was also about as much nutrient capital in the below-ground part of the ecosystem, and this is not depleted by logging. These figures are probably representative, though other data have not yet been gathered. They demonstrate that timber extraction by itself does not necessarily create a 'nutrient desert'.

The most serious effect on forest nutrients of logging is likely to result from damage to the soil surface because this causes disruption to the root layer, to seeds in the soil, to the roots and stems that provide sucker shoots, and to the decomposer community. All these sorts of damage will impair recovery of the ecosystem after logging, including nutrient uptake into the biomass. Where the top-soil is scraped off or excessively compacted the effects are strongest. On the Windsor Tableland

Table 8.4

*Estimates of dry weight and amounts of five major plant mineral nutrients in the bigger trees and in the whole above-ground biomass (lower montane rain forest at Kerigomna, New Guinea)*

| | Dry weight (t ha$^{-1}$) | Nutrient concentration (kg ha$^{-1}$) | | | | |
|---|---|---|---|---|---|---|
| | | N | P | Ca | Mg | K |
| Total above-ground biomass | 331 | 853 | 49 | 1490 | 212 | 699 |
| Trees $\geq$ 0.1 m diameter: | | | | | | |
| Total, | 295 | 585 | 30 | 1150 | 162 | 571 |
|   of which boles | 228 (77%) | 342 (59%) | 16 (54%) | 638 (56%) | 107 (66%) | 388 (68%) |
|   branches, twigs, and leaves | 67 | 243 | 14 | 515 | 55 | 183 |
| Per cent of total amount contained in boles $\geq$ 0.1 m diameter: | | | | | | |
| In wood and bark | 68% | 40% | 33% | 43% | 50% | 55% |
| In wood only | 61% | 25% | 23% | 12% | 38% | 41% |

From Grubb and Edwards (1982)

in north Queensland snig tracks showed losses of soil organic matter and plant nutrients which persisted for at least 4 years.[204]

A study of logging in Surinam[205] showed that heavy felling reduced evapotranspiration and there was a subsequent increase in nutrient leaching into streams because more of the incident rainfall ran down through the soil. By contrast, low intensity selective logging followed by refinement[206] did not result in increased nutrients in drainage water. This ecosystem was thus shown to be robust enough to withstand logging and silvicultural treatment up to a certain level but not beyond.

*Chips.* Clear felling and total utilization of all boles, limbs, and branches, including their bark, as a source of wood chips for paper manufacture is only taking place in three dryland tropical rain forests, Bajo Calima on the Pacific lowlands of Colombia, Gogol on the north coast of Papua New Guinea, and Sipitang in southwest Sabah. Careful study at Bajo Calima has shown complete recovery of the former amount of biomass by extremely vigorous and dense forest regeneration.[207] Here, extraction is by aerial cable to well-spaced roads and there is no damage to the forest floor, which after felling resembles on an extremely coarse scale the stubble left on a cereal field after the crop has been harvested. The secret of success probably lies in the mode of extraction adopted. No studies have been made, however, of biomass nutrients.

The original forest at Gogol was rich in pioneers and these regrow vigorously. At Sipitang the forest had been logged, it then burned in the Great Fire of Borneo (p. 117) and, after salvage harvesting for chips, plantations of *Acacia mangium* are being established. The consequent effects on ecosystem nutrients are being monitored.

*Fuelwood.* There are proposals that small remote towns in the Brazilian Amazon run their electric power stations on wood fuel. At present they use diesel oil which has to be imported to Manaus 1300 km inland and then brought on average 1000 km further by river. The rain forest can only provide fuelwood on a sustainable basis if ecosystem nutrients are not depleted by successive harvests. Would the return of furnace ash to the forest provide sufficient nutrients? Research is needed.

*Plantation forestry.* This also makes great demands on the ecosystem nutrient capital, because a high fraction of the above-ground biomass is removed as harvest at frequent intervals. This is shown in Table 8.5 for plantations of *Agathis dammara* and *Pinus merkusii* in central Java, grown on a 40- and 25-year rotation, respectively. It can be seen that harvesting of stems alone causes similar nutrient depletion, but when branches are also taken there is higher depletion at the *Agathis* site. When the whole biomass is removed depletion is

## Table 8.5
### Nutrient depletion by plantation trees, central Java

| | Nutrient concentration (kg ha$^{-1}$) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Co | | Mg | | K | | P | |
| **Agathis dammara over a 40-year rotation** | | | | | | | | |
| Inputs: | | | | | | | | |
| Atmosphere | 395 | | 160 | | 385 | | 35 | |
| Weathering rock | 3060 | | 1565 | | 1575 | | 200 | |
| Total inputs | 3455 | | 1725 | | 1960 | | 235 | |
| Outputs: | | | | | | | | |
| Stemwood harvest | 659 | 19% | 153 | 8% | 437 | 22% | 107 | 45% |
| Stem, branch and bark harvest[a] | 1679 | 48% | 329 | 19% | 854 | 43% | 204 | 87% |
| Total harvest of trees and undergrowth[b] | 3556 | 103% | 786 | 45% | 1894 | 97% | 372 | 158% |
| **Pinus merkusii over a 25-year rotation** | | | | | | | | |
| Inputs: | | | | | | | | |
| Atmosphere | 245 | | 70 | | 180 | | 70 | |
| Weathering rock | 1870 | | 965 | | 1015 | | 82 | |
| Total inputs | 2115 | | 1035 | | 1195 | | 152 | |
| Outputs: | | | | | | | | |
| Stemwood harvest | 413 | 19% | 97 | 1% | 219 | 18% | 73 | 48% |
| Stem and branch harvest | 672 | 32% | 127 | 12% | 274 | 23% | 83 | 55% |
| Total tree harvest[b] | 1558 | 74% | 266 | 26% | 666 | 56% | 134 | 88% |

Data from Bruijnzeel (1984, Table 4); Bruijnzeel and Wiersum (1985, Table 4)
[a] Bark used for fuel
[b] Twigs, leaves, and undergrowth used for animal bedding

higher still and at the *Agathis* site more is removed than the total inputs from both the atmosphere and rock weathering over the whole 40-year rotation. The soils here are andosols, derived from recent volcanic deposits, and unusually fertile (Table 8.1). On the far more extensive oxisols and ultisols soil nutrient capital is much less. One, or perhaps a few, successive, plantations may give reasonable economic yields. Nevertheless, there is no such thing as a 'free lunch' and the repeated harvesting of timber will inevitably sooner or later deplete ecosystem nutrients as more are removed than are added in rainfall. It is very likely that soil physical properties will also deteriorate. Studies on the nutrient capital in plantations are urgently needed, especially under second and later rotations.[208]

Besides potential problems of nutrient depletion, all plantation forests face the build-up of pests and diseases. These are especially troublesome in perhumid lowland tropical climates and were beginning to be serious at the extensive plantations at Jari in the lower Amazon by the mid 1980s, some 20 years after the venture started.[209]

Plantation forests on shallow, rejuvenating soils on hilly land may have a less serious nutrient problem, though they have problems of erosion and access for cultural and harvesting operations.

*Agriculture.* Conversion of rain forest to agriculture is even more extreme than conversion to plantation forests. Nutrient cycles are completely disrupted, especially uptake by plants and from decomposition. In a recent study at Yurimaguas in the Peruvian Amazon it has been found that the biomass of decomposers dropped from 54 to 3 g m$^{-1}$ in the conversion from rain forest to arable agriculture.[210]

Traditional agriculture of the shifting kind makes use of natural ecosystem processes, as described in section 8.1. There is scope for further enhancing the efficiency of the bush fallow period by planting species that are good 'nutrient pumps' from soil to biomass. It was found in the Philippines that *Trema orientalis* restores phosphorus and *Melastoma* cf. *polyanthum*, restores potassium to the above ground biomass.[211]

Continuous cultivation of short-lived crops is difficult to sustain without inputs of nutrients, though easier on more fertile soils. Experiments on ultisols at Yurimaguas showed that continuous cultivation of rice was not possible even with the addition of fertilizer, but yields could be maintained if crops were rotated, provided that fertilizers were added (Fig. 8.7). In Nigeria crop yields have proved sustainable for 10 years or more on small farms on alfisols (which are intrinsically more fertile than ultisols: Table 8.1) rotating maize, cowpea, cassava (*Zea mays*, *Vigna unguiculata*, *Manihot esculenta*), and a cover crop, with minimum tillage and the judicious addition of fertilizer.[212]

Oxisols and ultisols are the most widely occurring lowland tropical soils and amongst the least fertile (Table 8.1). It has been suggested for the Brazilian Amazon that conversion to agriculture should be confined to alfisols and to the alluvial soils that are found along the major rivers. The loss of alluvial, flood-plain swamp forests would, however, have serious consequences for the fish on which many people depend for a livelihood, as described on pp. 181–2.

*Agroforestry*. Mixed cultivation of trees with food crops is another possibility for maintaining yields (Fig. 8.8). This has been practised since time immemorial by peasant farmers, as for example the 'home gardens' of Central America, Java (Fig. 10.4), the Philippines, and Sumatra. Japanese immigrants living at Tomé Açu south of Belém in the Brazilian Amazon have developed over the last few decades a particularly intricate farming system which maintains continuous high production on infertile soils.[213] Fast-maturing food crops such as rice, maize and beans are interplanted with the slower maturing vines of pepper (*Piper nigrum*) and passion fruit (*Passiflora*) which are trained up tree crops such as cocoa, rubber, coconut, and *Astrocaryum* palm (grown for its edible apex, 'heart of palm'). Vanilla orchid (*Vanilla*), also a vine, is sometimes included. Some farmers specialize in chickens, whose waste, along with all other organic residues, is returned



**Fig. 8.7.** Agriculture on nutrient-poor lowland rain forest ultisols at Yurimaguas, Peru. (a) Yield is sustainable when crops are grown in rotation, but not (b) if rice is grown continuously. (After Jordan 1987, Figs. 6.10a, 6.11.)
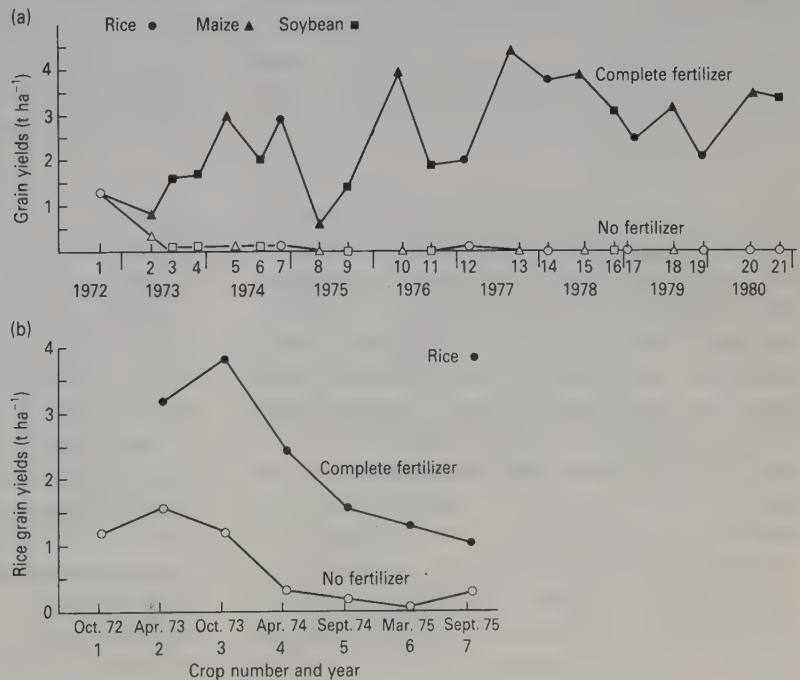
to the fields. Rotation and succession prevent build-up of pests and disease. The cultural discipline traditional to Japanese societies is important for the operation of this close-knit agricultural system.

In the 1980s mixed cultivation was 'discovered' by the aid agencies, who had become disillusioned with rain forest silviculture and tree plantations as vehicles for Third World development, and the term agroforestry was coined. The trees provide browse for domestic animals, fuelwood and lumber for buildings, and sometimes fruit as well. Agroforestry makes use of nutrient cycling by trees, as does shifting agriculture. Trees act as pumps, bringing nutrients into the superficial layers of the soil where shallow-rooted herbaceous crops can utilize them. Part of the nutrients comes via litterfall, and branches may be lopped and used as mulch to enhance this pathway. Part also comes from the decomposition of the fine roots of the trees. These are mycorrhizal and, in the case of Leguminosae and a few others, also have nitrogen-fixing nodules, so are particularly important in enhancing available phosphorus and nitrogen.

One agricultural system developed by agroforesters is so-called alley-cropping[214] where trees are planted as hedges with belts of food crops grown in the intervening lanes or alleys. There is still considerable scope for improvement of agroforestry. For example, tree species are needed which have deep roots and will act as good nutrient pumps on infertile oxisols and ultisols.



**Fig. 8.8.** Cultivation of crops in mixture in the Atlantic rain forest zone of Brazil. Here pineapple; and pepper, growing up the leguminous tree *Erythrina poeppigiana* which provides shade for cocoa; and the palm *Bactris gasipaes* are all being grown.

## 8.4. Heath forest—a fragile ecosystem[215]

Heath forest is perhaps the most distinctive and easily recognized of all the lowland rain forest formations. The soils are typical podzols. Below a superficial layer of peat or mor humus is a layer, sometimes several metres thick, of bleached white silica sand overlying a hard blackish humus-, or iron-pan. The forest itself has striking structure and physiognomy as described on pp. 18–21 and shown in Figs. 2.12, 2.13.

Heath forest sites cannot sustain agriculture. In Borneo this forest formation is called kerangas, land that will not grow rice. In Brazil the Rio Negro, which drains a huge area of heath forest, differs conspicuously from the rivers running through other kinds of forest in the virtual absence of riverine farming settlements. Until recently it was believed that heath forest soils were more infertile than others and that extreme oligotrophy (nutrient shortage) was the reason many heath forest plants have small very leathery leaves ('scleromorphic microphylls') and why crops cannot be grown on heath forest soils. Outside the tropics it has been known for many years that sclerophylly is associated with nutrient poverty, for example the shrubby forests around Sydney in eastern Australia and the shrublands that develop on

many north temperate peat bogs. The correlation between this physiognomic feature (one of the most striking attributes of heath forest), crop failure, and nutrient shortage seemed so rational that no one noticed that data on soil nutrients had not been collected. Furthermore, the Bornean heath forests have numerous pitcher plants (*Nepenthes*) and ant plants, groups that both have special means of obtaining nutrients. It seemed intuitively obvious that oligotrophy 'explained' the distinctive nature of heath forests; but intuition can be dangerously misleading in science. In 1958 P. W. Richards collected samples of heath forest soils and some adjacent ones from Brunei. The chemical analyses showed no great differences. This was so surprising that he said in his publication that he thought the samples must have become contaminated. The same results were obtained 20 years later in Kalimantan and at Mulu, Sarawak. All three data sets show that the soils under virgin heath forest are not systematically poorer in plant mineral nutrients than those under other forest formations close by. The same applies at the important San Carlos research area in southern Venezuela in the headwaters of the Rio Negro where in fact all formations occur on exceedingly infertile soils.[216] Virgin heath forest soils do, however, differ frm others in being unusually acidic, with pH less than 4.0, and to have low buffering capacity due to low concentrations of iron and aluminium sesquioxides. Phenols are abundant in heath forest leaves and litter, and these may be toxic or inhibit uptake when they leach into the soil.

Once heath forest is felled and burned the soil very quickly degenerates. The surface humus layer is either eroded, burned, or oxidized. The small amount of clay in the soil washes down the profile to leave almost pure silica sand, which unlike the clay and humus has no electrical charge to which nutrient ions can attach.[217] The soil may become even more acid. Without vegetation cover or a surface humus layer the white sand gets extremely hot in the sun. It now seems that this rapid and easy soil degradation is the reason why agriculture is impossible and why if heath forest is felled and burned it is replaced by bare sand with patches of shrubs or scattered trees, which are called padangs in the Eastern tropics and campinas in

Amazonia. Heath forests are a genuinely fragile ecosystem and are easily and irreversibly degraded by human disturbance. The removal of a very few trees per hectare for timber has proved a non-degrading form of utilization of heath forests on the east coast of Malaya. Under this light selective logging regime the forest canopy is scarcely opened and the soil surface only slightly disrupted. Here, man is working within the rather narrow limits that the fragile heath forest ecosystem can sustain.

Heath forests occur in perhumid tropical climates where dry seasons are absent or short and sporadic. It came as a revelation when in 1969 E. F. Brunig demonstrated for Sarawak, that, if instead of taking the rainfall for calendar months it was taken for successive 30-day periods through the year, and water balance was calculated, then heath forest sites can be seen to suffer periodic water shortage; this is especially seen for those near the coast which are under the influence of sea breezes which are somewhat desiccating. This is because the sandy heath forest soils are freely draining, have a low capacity to retain water, and are often shallow over the impermeable iron or humus pan. Similar periodic water shortage has been shown to occur even at San Carlos where mean annual rainfall is 3565 mm, and over 400 mm in all months except December and January when it is 150 mm. This is a very wet climate even by humid tropical standards. Nevertheless, dry spells of 3–6 days are not rare. Study has shown that during such dry spells the water-table falls. At San Carlos the heath forest occurs on low domelike hills and decreases in stature towards the summit, where the water-table drops furthest.

It now seems probable that the very striking characteristics of heath forest are most likely to be adaptations to survive drought periods, even if these are infrequent. The transpiration of water is a mechanism whereby leaves are kept cool, below the lethal temperature at which protoplasm denatures (i.e. their cells are literally cooked). A whole set of the physiognomic features of heath forest either minimize heat load or optimize cooling. This applies to highly reflective shiny or pale coloured leaves. Small leaves (which are so characteristic of this forest) have a greater air flow over them than large ones. Many species have the leaves held vertically or nearly so. At San Carlos

55 per cent of species have this adaptation and an excess of leaf temperature over the air of only 1.8–5.4°C. Experiments on the leaves of a number of species at Bako, Sarawak, found that the eight heath forest species investigated were no different in their ability to resist desiccation than those of adjacent evergreen rain forest. Other adaptations reduce water loss from the heath forest as a whole. These are the clustering of leaves, the clustering of leafy twigs into dense subcrowns, and perhaps also the very uniform forest canopy top surface which by its smoothness reduces turbulent mixing of air.

There still remains much research to conduct on heath forest to substantiate these indications.

For example, stature varies from only a few to over 30 m tall and the extent to which this is determined by water relations or by soil mineral nutrients is not known. Nor, at the extreme, is it known what determines the occurrence of natural open shrublands or grasslands. There is evidence at Mulu, Sarawak, that although the heath forest has about the same amount of litterfall as other formations nutrient concentrations in the litter are lower, which suggests the plants are retaining more of the nutrient capital, and this is most marked for nitrogen.

The heath forest formation is ripe for further studies on its water and nutrient relations to substantiate the fragmentary studies just described.

## 8.5.  The upper montane forest enigma

Besides the studies on heath forest discussed above there have also been considerable efforts to relate the special structural and physiognomic features of the upper montane rain forest formation to attributes of its habitat. As with heath forest the debate has centred on whether nutrient shortage or periodic drought are important.[218] Upper montane forest presents an additional problem that continues to puzzle scientists, namely that the montane forest zones (Fig. 2.7) all occur at higher elevations on big mountains than on small ones, the so-called *Massenerhebung* effect.

A general description of upper montane rain forest and its occurrence was given on pp. 15–18. In structure and physiognomy there are strong resemblances to heath forest and also with the open stunted form of peat swamp forest (p. 22). In Borneo and Malaya a few species occur in more than one of these formations. At its lower edge upper montane rain forest occurs only on ridge crests, interdigitated with the lower montane formation which penetrates upwards along valleys and slopes. The very lowest patches exist on raised knolls with the intervening cols occupied by lower montane forest. Crests and knolls are freely draining sites which receive water from rain but lose it by lateral movement in the soil. This outward movement of ground water carries soluble nutrients with it and, moreover, the soil

may dry out in spells of dry weather. Thus the sites of upper montane forest are both oligotrophic and drought-prone. As with heath forest it seems likely that either or both of these factors may determine the occurrence of upper montane forest, and which factor prevails on any given mountain can only be resolved by investigation. At one extreme the summit of Kolombangara, 1662 m, a small island in the Solomons has excessively impoverished soils, with continual nutrient leaching in a very wet climate (estimated rainfall 8250 mm). There is persistent cloud above 800 m. Oligotrophy is undoubtedly more important than periodic drought. At the other extreme the high, extinct, or quiescent volcanoes of west Java have young and relatively fertile volcanic soils, but drought occurs in all or most years and it is likely that periodic water stress is the more important factor.

The boundary between lower and upper montane rain forest is usually sharp with only a narrow blending zone (ecotone). This boundary often occurs at the bottom of the zone at which cloud habitually develops. Within the cloud the climate is extremely wet with moisture combed from the air by the trees, so-called fog-stripping. The leaf litter on the forest floor is sodden and anaerobic; decomposition is inhibited. Litter accumulates and eventually turns into peat. Bog moss (*Sphag-*

*num*) frequently grows in these waterlogged places and accentuates peat accumulation. Because there is very little decay, nutrients in the litter remain locked up in organic form and unavailable to plants. There are hints (p. 139) that nitrogen may be limiting. Where peat occurs certain upper montane tree species are favoured (including conifers and Myrtaceae) which are believed to facilitate peat development by having slowly decomposing litter. If this does occur, and the data from montane forests in Table 8.3 suggests it does, then the process of peat accumulation is self-reinforcing which will tend to sharpen the boundary with adjacent forests. The level at which the montane cloud-cap forms, and hence at which upper montane forest develops, depends on local and regional weather patterns. It is characteristically higher on large mountains so this is likely to be part of the cause of the *Massenerhebung* effect which, however, still evades complete explanation. Prolonged and detailed studies are needed to discover which environmental factors are most important in determining the forest zonation on any particular mountain. Drought may be rare and not detected by a short period of study but, as with heath forest, upper montane species must be adapted to survive even rare droughts.[219]

Montane forest zones provide excellent opportunities for the study of plant-environment interactions, especially in water relations and mineral nutrition. One of the difficulties in understanding the root causes of zonation, the complete change in structure and physiognomy, and a concomitant reduction in forest biomass, is that different species grow at different elevations. A potentially powerful but yet undeveloped avenue of research is to investigate those few species that grow in several different montane forest formations, or to work on a small mountain, such as Rakata Island (735 m altitude) in the Krakatau archipelago between Java and Sumatra, which has the same flora from sea-level to summit yet whose forests become stunted upwards.

## 8.6. Nutrients and their cycles—Chapter summary

1. Shifting agriculture has been invented independently in all parts of the tropics and has proved sustainable since time immemorial. It is a low input system, suitable for infertile rain forest soils. Crops are grown for one or two years and then secondary forest, 'bush fallow', allowed to grow for 8–10 years or more.

2. Shifting agriculture works by using the capacity of trees to grow on acid infertile soils and bring nutrients from the soil into the biomass. During the bush fallow period nutrients re-accumulate in the vegetation (Fig. 8.4), partly from the soil, partly from rain. Crops cannot be grown for long because the soil becomes impoverished and acid, and pests, diseases, and weeds increase.

3. Shifting agriculture breaks down if cultivation continues too long or the bush fallow is too short. This happens, for example, when population increases too much or when it is practised by unskilled farmers.

4. In many tropical rain forests, most nutrients are fairly evenly divided between above- and below-ground parts of the ecosystem (Fig. 8.5), not nearly all above ground as formerly believed.

5. Nutrients are added to all forests in rain, both in solution and as aerosols. Forests on young, shallow soils also receive nutrients from decomposing rock, but on old, deep soils the soil parent material is beyond the reach of roots, there is no nutrient addition, and these soils are commonly less fertile (Table 8.2).

6. Nutrients cycle through the ecosystem (Fig. 8.6). Rain, as canopy throughfall, and litterfall are the main pathways. Fine litter decomposes in a year or less (Table 8.3). Soil invertebrates are important litter decomposers. In the lowlands termites predominate.

7. Sustainable utilization depends on working within the limits of ecosystem nutrient cycles. Shifting agriculture and selective removal of trees for timber do not cause serious permanent depletion (Fig. 8.4, Table 8.4). More complete biomass utilization for wood chips or in plantation forestry (Table 8.5) will deplete ecosystem nutrients un-

less balanced by rain and soil inputs. These prac-
tices may also disrupt the forest floor, and hence
the capacity for litter breakdown and forest re-
generation.

8. Permanent agriculture destroys forest eco-
system processes and requires addition of fertil-
izers (Fig. 8.7). The mixed cultivation of trees and
crops, agroforestry (Fig. 8.8), uses the nutrient
cycling capacity of trees for agricultural purposes.

# Species richness

One of the most famous features of tropical rain forests is their extreme species richness which has impressed scientists ever since the earliest explorations (Chapter 1). As has been described above (p. 29), in the richest rain forests every second tree on a hectare or so is a different species; even disregarding the trees some rain forests are richer in species than any other vegetation on earth; and the richest communities outside the humid tropics have about the same total number of species on small plots as there are trees of 0.1 m in diameter and greater in many rain forests. The way such very large numbers of species have evolved and are packed together has been the driving force for endless speculation, constrained to varying degrees by observation, and commonly involving massive extrapolation. It is one of the most basic and fascinating aspects of these forests and one that energizes much of tropical biology. Given the complexity and diversity of tropical rain forests generalization can be dangerous. Species richness has numerous components, many of which have been discussed in preceding chapters. Here all the different factors that collectively contribute to species richness are brought together. Concerning animals, the ways numerous species coexist, and limits to the carrying capacity of the forest have already been considered in Chapter 4. In this chapter we concentrate on plants.[220] Some of the factors described apply equally to animals.

## Historical plant geography

Extreme floristic richness involves the co-occurrence of a large number of species drawn from many genera and families. In the ultimate analysis, a region contains only those species that immigration and evolution, plus survival, have enabled to be present.

In Chapter 6 two aspects of historical biogeography were discussed which have importance for patterns of species richness today, namely evolution on the fragments of Laurasia and Gondwanaland and, more recently, fluctuations in climate. For example, a factor contributing to the floristic richness of the Eastern tropics is that taxa of both Gondwanan and Laurasian origin are intermingled. The poor rain forest flora of Africa is believed to be due to stronger desiccation and consequent heavier extinction than has occurred in the other tropical regions.

The African rain forests today have three zones with higher species richness (Fig. 6.17). These are thought to be places that were least affected by the drier, more seasonal climates of successive Pleistocene Glacial epochs. In tropical America also a series of areas of high endemism and species richness have been detected for many different groups of animals and those families of flowering plants that have been analysed (Fig. 6.16). The areas of endemism and richness are more or less coincident for different groups. As in Africa they are believe to be Pleistocene refugia to which rain forests and their component biota were confined at Glacial maxima. In South America the physical environment between refugia bears geoscientific evidence of past seasonality in the climate, which strengthens the argument that rain forests became like islands in a sea of seasonal forest. The Eastern tropics are species rich, with high local endemism. Unlike Africa and America there are no zones of relative poverty. It was shown in Chapter 6 that this is probably because the relatively species-poor regions have been drowned by rising sea-levels since the end of the last Glaciation.

In Africa tree species numbers on small plots are highest in the refugia. There are too few counts yet from the Amazon basin for a pattern to

be detected. It can be predicted that there too tree species richness is greatest in refugia.

Temperate forests also have patterns of varying floristic richness which are explicable in terms of past climatic history, as discussed on p. 96.

### Species niches in the forest

Given a rich regional flora, forests are particularly favourable for the coexistence of many species in the same community, because they provide many different niches.

*The forest canopy.* The forest provides a wide array of different internal microclimates, both horizontally and vertically (section 7.1). There are tree species with different degrees of shade tolerance. The trees themselves are the framework of a wide series of habitats for climbers and epiphytes (Fig. 9.1).

*The forest growth cycle.* This provides another set of niches, as described in Chapters 2 and 7. Big gaps are colonized by well-dispersed, light-demanding tree species which are eventually replaced by shade-bearers. There are many differences between species in fruiting frequency, dispersal efficiency, germination, seedling survival and establishment, and light requirements of juveniles. The same processes operate in all forests but forests have different degrees of complexity in canopy structure and differ in the number of species that occupy the many facets of what may be termed the 'regeneration niche'.

*Site.* The forest growth cycle interacts with differences between tree species in response to soil, drainage, and slope (section 2.5).

Thus, in any area we can expect to find a mosaic of patches of different species resultant from the operation of the forest growth cycle, superim-



**Fig. 9.1.** Luxuriant riverine rain forest near Rio de Janeiro with a wealth of species. (von Martius 1840 plate XIII.)
The spiny palm is a *Bactris*. The epiphytes are mostly aroids: top left *Philodendron* sp. (long stem), below it *Anthurium solitarium* (huge rosette), on right hand tree *A. harrisii* (lanceolate leaves), and *A. pentaphyllum* (palmately compound leaves). Other epiphytes are bromeliads (spiny leaf margins) and orchids (seen flowering). On the ground are two more aroids *Philodendron martianum* (below, huge rosette) and *P. speciosum* (cordate leaves, centre).

posed on a patchiness resultant from the varied response of different species to site factors. The forest will be still more intricate if there are several species equally well suited to these various niches. Around the trees the herbs and dependent synusiae colonize and compete in a similar complex manner.

*Forest formations.* At a broader scale of site different forest formations occupy different habitats and many species are confined to one or only a few formations.

## Interactions between plants and animals

In Chapter 5 the various syndromes of characters of flower and fruit were discussed which have evolved to attract particular pollinating or dispersing animals, and this diversity of food sources is one of the factors underlying animal species richness (section 4.2). It seems that one-to-one specialization between a single plant and animal species as a factor of species richness only exists in a few cases, such as figs (Fig. 5.14). Guilds of insects specialized to feed on (and where necessary detoxify) particular families or similar families of plants (which are sometimes called plant webs) is a looser and commoner form of co-evolution and plays a more substantial role in the packing together of numerous sympatric species (section 5.4).

In the humid tropics flowering, fruiting, and germination are possible throughout the year. Species dependent on animals for pollination or dispersal may have a better chance of success if they do not compete with others for the services of animals. This can lead to phenological separation by staggered flowering or fruiting times; examples were given in Figs. 5.7, 5.8. West Malesian Dipterocarpaceae are interesting: staggered flowering times have evolved which maximize the chance of any individual species successfully cross-pollinating, but the different species then all reach fruit maturity simultaneously which satiates predators and maximizes the chance of successful germination.

Browsing pressure ('pest pressure') of herbivores (p. 74) may be one factor that sometimes prevents any single species from attaining domin-

ance, and acts to maintain species richness. In a similar manner dense seedling populations below a parent tree are often thinned out by disease or herbivory (section 7.3) and this also therefore contributes to the prevention of single species dominance.

## Evolution

Most botanists believe that genera and families originate by a continuation of the processes of evolution by natural selection which lead to the evolution of species. It can be argued that the flora of a region continues to evolve new species which therefore accumulate with time. Highly stable areas come to develop a rich flora because there is little extinction. In the humid tropics the accumulation of species is accentuated because survival is not limited by a cold or dry season acting as a 'climatic sieve' and so extinction is even lower than in stable parts of other biomes.

The most species-rich plot so far enumerated is in Peru with 283 species of trees 0.1 m in diameter or over amongst 580 stems on one hectare (Fig. 2.27). Here, every second tree is a different species. Several plots in Borneo are almost as rich. These forests may be near the upper limit possible for sustainable tree species richness. Over the medium and long time-scale, species need to outbreed to counteract the effect of accumulating deleterious mutations and in order to express the genetic variability on which natural selection then operates. In this way the species keeps highly adapted to competition and climate as these change. For outbreeding several individuals need to exist close enough to cross-pollinate. It would be interesting in these hyper-rich forests to examine the species-area curve, to see if species numbers continue to rise beyond one hectare, and also to study the distance of effective cross-pollination.

Evolution may eventually led to the co-occurrence of series of sympatric species. In the temperate forests of east Asia and north America this is well shown by *Acer* and *Quercus*. There are many examples in lowland tropical rain forests, see p. 78.

Long series of sympatric species are found in many parts of the world. Not all are forest trees and the evolutionary origin is not always the

same. In southern Africa there are swarms of several hundred *Erica* species in the Cape heathlands and of many dozens of *Mesembryanthemum* in Botswana. In mid-northern latitudes *Crataegus*, *Hieracium*, and *Rubus* (hawthorn, hawkweed, blackberry) are examples. The high mountain forests of Malesia, especially New Guinea, have many sympatric orchids (*Bulbophyllum, Dendrobium*) and Ericaceae (*Rhododendron, Vaccinium*). There are 16 sympatric pitcher plant species (*Nepenthes*) on Mt. Kinabalu in Borneo.

An important difference of tropical rain forests from others is the occurrence of locally endemic species (p. 29). This is one component of their species richness on the extensive scale. It means that in different places a particular niche may be occupied by different species which never compete because they never meet. It has the consequence that species are likely to become extinct when a rain forest is reduced in extent, more so than in other forest biomes.

Study of breeding systems in rain forest plants has shown that these are as diverse as in other biomes. No particular breeding system predominates to act as the driving force behind speciation.

### Conclusions and summary

There are thus many different components to species richness, and many different causes. It is necessary in any discussion to specify the scale, whether local or regional, as discussed on p. 29. It is not easy to discover whether there are species of identical ecology, i.e. which occupy the same niche. Many species of *Shorea* growing together in Pasoh forest, Malaya, have not been demonstrated to have different site requirements and it seems likely that the manifold roles of chance are important there (and elsewhere) in determining forest composition.

In summary, the main reasons why some tropical rain forests are extremely rich in species results from firstly, a long stable climatic history without episodes of extinction, in an equable environment, and in which there is no 'climatic sieve' to eliminate some species. Secondly, a forest canopy provides large numbers of spatial and temporal niches; the forest growth cycle is important here. Thirdly, richness results from interactions with animals, mainly as pollinators, dispersers, or pests. Some of these factors underly species richness in other biomes also.

The American forest ecologist R. H. Whittaker[221] can be allowed the final word on this subject. From the analysis of this chapter we may agree with his statement that 'the study of diversity has revealed divergent relationships in different groups and places and these are subject much less to prediction than to observation and evolutionary interpretation'.

The overall effect of all of Mankind's many different impacts on tropical rain forests is to diminish the numerous dimensions of species richness. Not only does man destroy species, he also simplifies the ecosystems the remaining species inhabit. It is to this serious contemporary subject that we now turn in the final chapter.

# 10

# Tropical rain forests yesterday, today, and tomorrow

The dominant image of the age in which we live is that of the earth rising above the horizon of the moon—a beautiful, fragile sphere which provides the home and sustains the life of the entire human species.[222]

Modern man, especially where living in comparative luxury in more or less democratic societies, has developed a conscience about the destructive exploitation of the planet's resources for which he is largely responsible, and a concern that the human species has come to live beyond the resources of 'spaceship Earth'.[223] The problem of disequilibrium has become acute as human numbers have dramatically increased (Fig. 10.1). The increase is mostly in the tropics and sub-tropics where the demographic transition to small families typical of industrialized communities is only now patchily beginning to take place. The impact of all these people is exacerbated by bigger economic aspirations and consequent greater demands per person on the environment. Tropical rain forests are one of the last great forest frontiers to be rolled back by the human species.[224] The temperate forests of Europe and China were reduced to only a small fraction of their post-Glacial natural extent over the past two millenia. England was in fact less forested at Domesday (1086 AD) than now. Later, the temperate forests of North America were hard hit by European immigrants. With the advent of modern hauling machinery, bulldozers, skidders, and chain-saws, man is now attacking the tropical rain forest. This time forest destruction is taking place much more rapidly. The markets are largely in industrialized nations. For example, much dipterocarp timber from southeast Asia ends up as plywood houses in western North America.[225] Considerable funds for roads, dams, and mines come from the industrial nations, so concern within these nations about
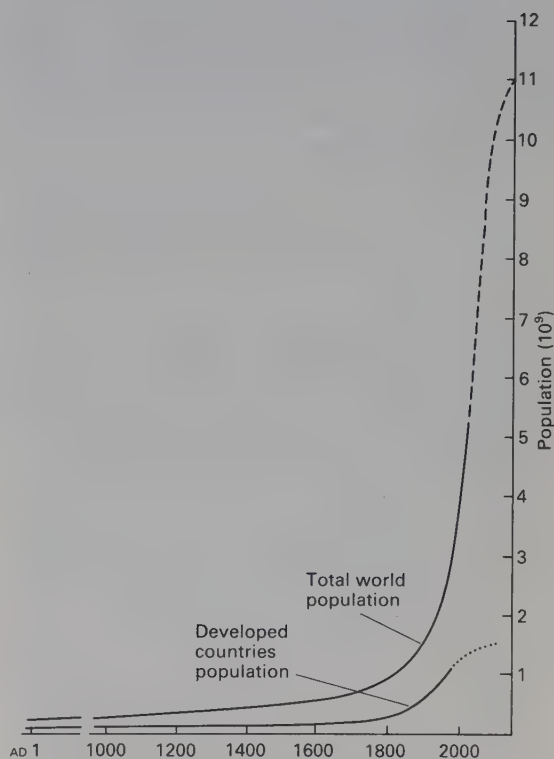


**Fig. 10.1.** Human population numbers. (World Bank figures cited in Anon. 1985.)

The world population doubled between 1650 and 1850. The most recent doubling took only 44 years, and a total population of $5 \times 10^9$ was reached by mid 1987. It is predicted that the next doubling will occur in 49 years and in Africa in 25 years, and maybe even sooner. If very stern population control measures were initiated now, global human population might stabilize at $c.\ 8 \times 10^9$ by the 21st century, but $11 \times 10^9$ is a more likely total.

their complicity with rain forest destruction is certainly fully justified. The rain forest countries

need the money released by the sale of timber, and need forest land for people, for food production, and for plantations which if well managed put money in the bank at a greater rate than natural forests ever can.

Developed nations on their own, or in partnership in consortia such as the European Community or World Bank, give or lend money and the expertise and machinery it buys—bilateral and multilateral aid.[226] Economists are called in. To them virgin forests represent so much standing timber, capital not earning interest and which should be liquidated.

This scenario is over-simplistic, but shows the basic mechanisms of the complete switch from traditional use of the forests under social control for innumerable 'goods and services', to their use today as timber mines.

Foresters, and standing behind them ecologists, are well aware that forests are naturally under continuous renewal and that if man works within the limits of the ecosystem they are a continually replaceable resource. Effective silvicultural systems have been devised for many tropical rain forests and enough is known to devise them for most others.

However, foresters who work with tropical rain forests have to a large extent failed.[227] In the whole humid tropics there are only a handful of examples where the forests are being used as a timber resource on a renewable basis. Management of forests only works where there is the political will. Human cupidity has nearly everywhere overturned the rules tropical foresters have devised. As a profession they have failed to come to terms with and to contain this basic aspect of man's nature, tending instead to throw up their hands in horror. The logging concessionaire pays lip service or less to the rules because he wrongly thinks it would cost more money to follow them (p. 123), and he has only been given a short-term licence to cut, so he will not be there next cycle. He is allowed to break the silvicultural rules because he has paid the politician to gain the concession, or he may be a politician himself. The nation received foreign aid money to build the main access highways because aid agency economists deemed the country needed to mobilize the capital its forests contain and because bankers deemed the country was a good risk and would pay the interest and not default on the loan. Foresters have proved totally powerless in the face of this cabal.

Fortunately, many aid-giving nations are subject to democratic pressures and there has been a burgeoning of what are known as NGOs, Non-Governmental Organizations, focusing on rain forests. Doyen amongst them is the International Union for Conservation of Nature (IUCN) and its offshoot the World Wildlife Fund (WWF).[228] Prominent amongst others are Friends of the Earth, Survival International, Greenpeace, and the World Resources Institute. On a national level may be mentioned the Malayan Nature Society, national branches of World Wildlife Fund and the Rain Forest Conservation Society of Queensland, to name just a few.

These NGOs have in recent years begun to force aid agencies to build in controls to minimize environmental damage, which however are unfortunately not always obeyed. The NGOs also hope to turn the page of history back from the very recent sole emphasis on rain forests as sources of timber to their conservation and sustainable exploitation for a multitude of products and as providers of so-called 'services'.

In this final chapter we take a brief look at these complicated issues. The development of man's use of tropical rain forests is traced, modern impacts and the reasons for concern are briefly examined,[229] and then the contemporary seeds of change are described.

## 10.1. Indigenous cultures

Human societies in rain forest lands developed in various ways, some of which persist today, though with increasing interference from the outside world.[230]

Hunter-gatherer societies live in all three rain forest regions. In central Africa are the Mbuti, in the Amazonian forests many small groups of Amerindians, a few still with little or no contact

with the outside world, and in the Eastern rain forests tribes such as the Onge and Jarawa of the South Andaman Islands,[231] and the Penan of northern Sarawak and Brunei. These peoples have an intimate knowledge of the forest and do not destroy it.

Settled agriculture long ago led to the permanent clearance of parts of the rain forest. The freshwater swamp forests (p. 22) of the alluvial plains of Asia were replaced by irrigated rice, a highly labour-intensive crop that can support very dense human populations, for example 2500 km$^{-2}$ on the Tonkin delta. In some places settled agricultural societies have disappeared and land reverted to forest. This has happened in middle America where traces of Aztec and Mayan agriculture persist as forests very rich in fruit trees in regions where the first Spanish explorers recorded open country, and where also forests have regrown on land the European settlers cleared for cattle. In Sri Lanka, and in Cambodia at Angkor, the ruins of irrigation systems and buildings (Fig. 10.2) occur within tall species-rich forest.[232]

The most extensive farming in rain forests was by shifting agriculture, which developed in all parts of the tropics (Fig. 10.3). This was described in Chapter 8, where it was shown that, if practised carefully, shifting agriculture is a sustainable mode of cultivation, well-adapted to infertile soils. Shifting agriculture can usually only support 10–20 persons (Table 10.1).

These traditional human societies make use of many sorts of plants, most of them wild. Settled agriculturists plant orchards of mixed species of trees and also many climbers and herbs for timber, food, cordage, and medicines (Figs. 8.8, 10.4). Some are wild species, others known only in cultivation (Table 10.2). Bantor Kalong, a village in west Java, was found in the 1970s to have 425 plant species in cultivation.

Shifting farmers commonly leave patches of primary forest intact to retain useful plants and as

a habitat for the animals they hunt for meat. In addition many species of the secondary forest fallow (sometimes called the bush fallow) are utilized

### Table 10.1
*Population density of shifting agriculturists in various Malesian rain forests*

| | | Persons (km$^{-2}$) | Fallow period (years) |
|---|---|---|---|
| Borneo | | | |
| Kalimantan | Kantu[a] | 16 | 7 |
| Sarawak | Kenyah[b] | 11–18 | 20–12 |
| | Iban[c] | 18 | 12 |
| Philippines | Hanunoo[d] | 48 | 12 |
| New Guinea | Tsembaga[e] | 34 | 15–25 |

The calculations assume 50–70% of the land is cultivable

[a] Dove (1981)
[b] Chin (1985)
[c] Freeman (1955) in Chin (1985)
[d] Conklin (1957)
[e] Rappaport (1967, 1971)
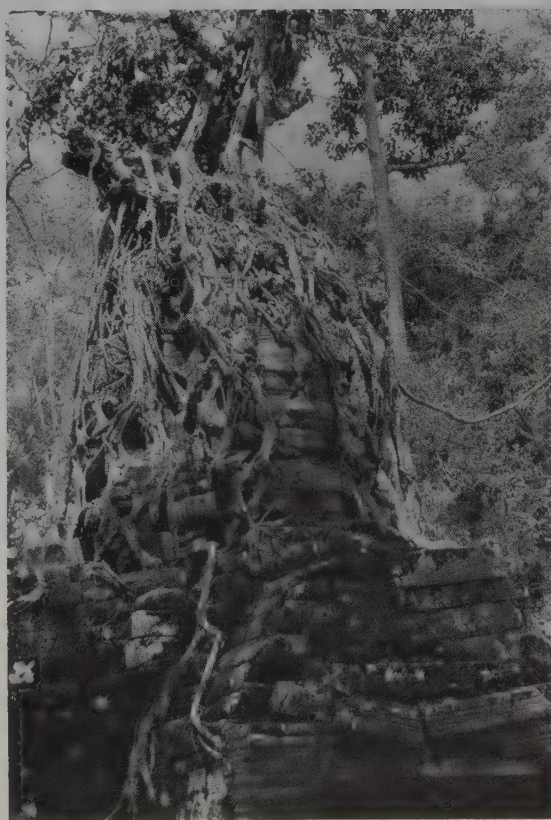


**Fig. 10.2.** A strangling fig growing over a Hindu stupa at the huge temple complex of Angkor Wat, Cambodia, which was built during the 10th–12th centuries and abandoned in the 15th century when the Khmer civilization collapsed. It was reclaimed from the jungle in the late 19th century by the then French rulers of Indo-China.

## Table 10.2
### *Cultivated plants at Kampong Melor, Malaya*

Staple food plants:
  New World origin
    *Manihot esculenta*
    *Zea mays*
Fruit trees:
  (a) Cultivated, also found wild in rain forest
    *Artocarpus integer*
    *Baccaurea griffithii*
    *B. motleyana*
    *Bouea macrophylla*
    *Durio malaccensis*
    *Garcinia atroviridis*
    *Nephelium lappaceum*
    *N. ramboutan-ake*
    *Pangium edule*
    *Parkia speciosa*
    *Pithecellobium (Archidendron) jiringa*
    *Sandoricum koetjape* (sentul)
  (b) Cultivated, wild ancestors of same species in
      adjacent rain forest
    3 *Eugenia* spp.
    *Lansium domesticum*
    *Mangifera* sp.
    *Sandoricum koetjape* (sertapi)
  (c) Cultivated, indigenous to the tropical Far East,
      but wild ancestors unknown
    *Areca catechu*
    *Artocarpus heterophyllus*
    *Cocos nucifera*
    *Durio zibethinus*
    *Garcinia mangostana*
  (d) Introduced, all from the New World
    *Annona muricata*
    *Averrhoa bilimbi*
    *Carica papaya*

Data compiled by the author on a short visit on 2 July 1971

(Table 10.3), and species may be planted that attract game animals.

Recent investigations in the Amazon have found forests rich in useful species, some growing outside their natural geographical range. For example, an inventory of 1 ha of tall uninhabited forest near the river Xingu in Brazil found 147 tree species of 0.1 m in diameter or over. Three of the ten dominants were food trees (the palm babassù, *Orbignya phalerata*, *Inga*, and a cocoa relative) and many of the other species were also useful, e.g. Brazil nut (*Bertholletia excelsa*). It seems likely that this forest has been augmented by former human inhabitants, either shifting cultivators or hunter-gatherers, who have since died out; another forest nearby had only 100–120 species ha⁻¹, and lacked the useful ones.[233]

Utilization of the resources of the forest by these traditional societies is under strong social controls which prevent over-exploitation, as only a sustainable harvest is gathered. This is the case, for example, of the wild sago palm *Eugeissona utilis*, staple food of the Sarawak nomadic Penan; and of minor forest products, mainly rattans and resins, traded far downriver for kerosene, cloth, and steel tools, from the remote Apo Kayan region of northeast Kalimantan.[234]

Strong trade links have existed for two millenia between southeast Asia and China. Borneo, for example, bartered hornbill ivory, bezoar stones, gaharu (eaglewood, diseased heartwood of *Aquilaria malaccensis* used for incense), kingfisher feathers, turtle eggs, damar (resin from *Agathis*, Burseraceae, and Dipterocarpaceae), camphor (from *Dryobalanops*), dragon's blood (fruit surface resin of certain rattan palms), and edible birds' nests, for ceramics, which have become heirlooms and symbols of wealth.

## 10.2. The colonial era

European exploration of the world and later settlement had a profound effect throughout the humid tropics.

European interest in tropical rain forests was at first focused on them as the source of spices, especially important before refrigeration to mask the flavour of preserved meat. The New World was discovered during the search for a better route to the Spice Islands of the East Indies, present day Maluku (the Moluccas). It is no exaggeration to say that nutmeg, cloves and pepper (*Myristica fragrans*, *Syzygium aromaticum*, *Piper nigrum*) have shaped the history of the world. Trade for spices was soon followed by settlement, to consolidate,

Table 10.3

*Useful plants in the fields and forest fallows of Bora Indian shifting agriculture, Amazonian Peru*

| Stage | Planted | Spontaneous |
|---|---|---|
| High forest | — | Numerous species for construction, medicine, handicrafts, and food |
| Newly planted field, 0–3 months | — | Dry firewood from unburnt trees for hot fires |
| New field, 3–9 months | Corn, rice, cowpeas (*Vigna unguiculata*) | Various early successional species |
| Mature field, 9 months – 2 years | Manioc[b], some tubers[b], bananas[a,b], cocona (*Solanum sessiliflorum*)[a], and other quick maturing crops | Vines and herbs of forest edges |
| Transitional field, 1–5 years. Seedlings of useful trees appear | Replanted manioc, pineapples[a], peanuts[a], coca, guava[b], caimito (*Pouteria caimito*)[a], uvilla (*Pourouma cecropiifolia*)[a], avocado[a], cashew[a], barbasco (*Lonchocarpus nicou*)[a], peppers (*Capsicum*)[a], tubers; trapped game | Medicinal plants within field and on edges. Abandoned edges yield straight, tall saplings, including *Cecropia* and *Ochroma lagopus* |
| Transitional fruit field, 4–6 years, with abundant forest regrowth | Peach palm (*Bactris gasipaes*)[a], banana, uvilla, caimito, guava, annatto (*Bixa orellana*), coca, some tubers; propagules of pineapples and other crops; hunted and trapped game | Many useful soft construction woods and firewoods. Palms appear, including *Astrocaryum*[d]. Many vines; useful understorey aroids |
| Orchard fallow, 6–12 years | Peach palm, some uvilla, macambo (*Theobroma bicolor*)[a]; hunted game | Useful plants as above; self-seeding *Inga*. Probably most productive fallow stage |
| Forest fallow, 12–30 | Macambo, umari (*Poraqueiba sericea*)[a], breadfruit[a], copal (*Dacryodes* sp.) | Self-seeding macambo and umari. Some hardwoods becoming harvestable, e.g., cumala. Many large palms: huicungo (*Astrocaryum huicungo*), chambira (*A. chambira*), assai (*Euterpe* sp.), ungurahui (*Jessenia bataua*)[d] |
| Old fallow, high forest over 30 years | Umari, macambo | A few residual planted and managed trees |

From table 1, Denevan *et al.* in Lugo *et al.* (1987)

[a] Fruits
[b] Carbohydrates
[c] Fish poison
[d] Oil
Other species mainly for medicinal or utilitarian uses

control, and increase the supply. The Dutch, who monopolized the trade in nutmeg from the mid 17th to early 19th century, restricted its cultivation by force to Ambon and Banda, small islands in Maluku, destroying the trees on other islands; but they were thwarted by pigeons which as specialized frugivores dispersed the seeds.[235] Still today the primitive cultivars of cloves are difficult to

**Fig. 10.3.** Shifting agriculture in the Atlantic coast rain forest of Brazil near Rio de Janeiro in the early 19th century. The huge tree on the left is a *Ficus*. (von Martius 1840, plate XVI.)

locate because the Dutch only permitted cultivation on Ambon, and plantations elsewhere were destroyed.

The trading posts were followed by full colonial domination. With it the European powers began the movement of useful plants between the different tropical regions. Captain Cook and other voyagers brought back descriptions from Polynesia of the tree from which 'bread itself is gathered as a fruit' and Lieutenant William Bligh was conveying breadfruit (*Artocarpus altilis*) from Tahiti to the Caribbean on the Bounty when his crew mutinied on 28 April 1789. Botanic Gardens were established as centres for plant introduction and trial, for example Peradeniya in Sri Lanka, Singapore, Bogor in Java, Rio de Janeiro, and St. Vincent in the Caribbean (where the original

breadfruit tree planted after Bligh's second voyage in 1793 still stands). Weeds were inadvertently transported, often in ships' ballast. The first New World weeds to reach Asia arrived via the Spanish galleon route between Acapulco in Mexico and Manila in the Philippines.[236] Their spread through the Malay archipelago can be traced outwards from Manila. Until the age of European expansion no cultivated plant was pantropical. Today even traditional societies extensively cultivate species that originated in another continent, bananas (*Musa*, from Asia), and cassava, maize, and sweet potatoes (*Manihot esculenta*, *Zea mays*, *Ipomoea batatas*, from America) are major examples; see also Table 10.2. In the highlands of Papua New Guinea a population explosion followed the introduction to Asia from South America of

**Fig. 10.4.** A Javanese village set amongst useful trees. Left to right: durian (in fruit), sugar palm (*Arenga pinnata*), coconut, two betel nut palms (*Areca catechu*), sugar palm, and kapok. (Blume 1835, plate 104.)

This is the cultivated variety of kapok, *Ceiba pentandra* var. *pentandra* cf. Figs. 1.6, 3.30.

sweet potato by the Spaniards; previously no high-yielding staple food occurred that could be grown at such high altitude.

The Industrial Revolution increased demand for tropical products. By the late nineteenth century plantations had been established, for example in Asia to produce para rubber, an Amazonian species (*Hevea brasiliensis*), plus the indigenous gutta-percha (*Palaquium gutta*) (cf. p. 118) and gambir (*Uncaria gambir*) for tannin, as well as food crops, beverages (tea, coffee, cocoa: *Thea sinensis*, *Coffea* spp., *Theobroma cacao*) and spices. The rain forests also provided industrial raw materials, gathered by forest dwellers and traded through middlemen to the great entrepôts such as Manaus and Belém on the Amazon, Makassar,

and Singapore. Over-exploitation sometimes occurred. Where the market was strong social controls on occasion broke down. For example, the conifers *Agathis* produce Manila copal, a resin used in varnishes and formerly also in linoleum. There had always been a small trade as the resin is also used in batik cloth manufacture and for torches and boat caulking. The high European demand led to increased and destructive tapping so that many trees were killed in the *Agathis* forests of central Indonesia (Fig. 10.5). The colonial administration of the Dutch East Indies introduced regulations that attempted to prevent this and other over-exploitation.[237]

Forest Departments were established and Forest Reserves created. In the British Empire
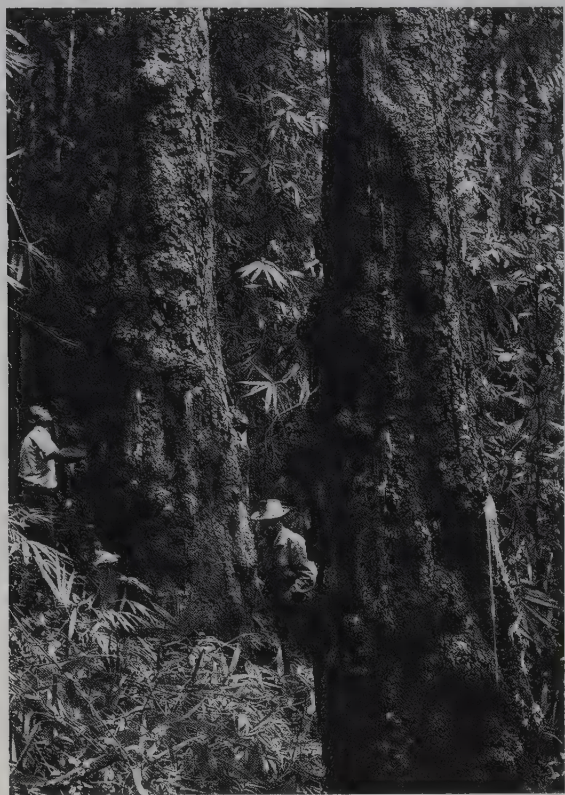
**Fig. 10.5.** *Agathis dammara* tapped for the resin in its bark which is traded as Manila Copal. Sulawesi. (Whitmore 1980, Fig. 6.)

The trunk has been damaged by excessively large tapping scars.

the officers were called Forest Conservators. The survival today of 71 ha of partly primary rain forest at Bukit Timah on Singapore, a tiny City State of 2.6 million people on 622 km$^2$, and of 1 million ha of an original 1.2 million ha of the Queensland rain forests, is testimony to the ethos of the conservative colonial era.[238] Figure 10.6 shows how the only remaining tropical moist forests in Ghana survive as Forest Reserves created by the former colonial government, and set today in a sea of dense agricultural settlement.

A consequence of European impact on the humid tropics, whose full extent is only now coming to be discovered, was the total disruption and in places the extirpation of whole societies of indigenous people. The Amerindian population of the New World rain forests collapsed as tribes

succumbed to introduced respiratory diseases and measles. Today the Amazon basin has only about 4 per cent of its former indigenous population.[239] Those who remain are mostly hunter-gatherers and fishermen. There is far less shifting agriculture practised there today. Current botanical investigations are finding many traces in forest composition and structure of former forest destruction by farmers. Some were mentioned above but the most dramatic example is the discovery that babassu palm (*Orbignya phalerata*) owes its abundance and extensive range to man.[240] Babassu is dominant or common in huge areas of the Brazilian Amazon (Fig. 10.7). Dense seedling carpets form (over 6000 ha$^{-1}$) and persist in forest shade. The young plant has a subterranean growing point and can survive fire. The palm can live for nearly 200 years. It has many useful products for sale and subsistence and is a major component of the rural economy in Maranhão state in the lower Amazon. The kernel is rich in protein and contains an edible oil which is also an effective insect repellent and is used for soap manufacture; the mesocarp is rich in starch and made into flour; the fronds and trunk are used for palm heart, thatch, baskets, mats, fans, sieves, rails, bridges, and foundations. Beetle grubs which feed on the apex are edible and also produce a fat used for lubricating hunting bows. Another important sign of the former denser populations of Amazonia are the areas of black soil, *terra preta*, mostly *c.* 4 ha in extent, which contain potsherds and are of anthropogenic origin. *Terra preta* is fertile and is preferentially used for agriculture by contemporary inhabitants. The very extensive climber-dominated forests of the Amazon may also have an anthropogenic origin.

In other parts of the humid tropics it is being discovered that human societies also formerly lived in places covered today (or until recently) with what everyone had believed was primary, virgin, rain forest. Much of the rain forest of middle America is on sites that were open farmland at the time of the Spanish Conquest (p. 155). The Okomu forest of Nigeria has signs of former villages in its soil, and is believed to be several-century-old regrowth (p. 130). Old secondary forest is extensive in Borneo, New Guinea and the Solomons with past farming as one possible explanation. Fruit
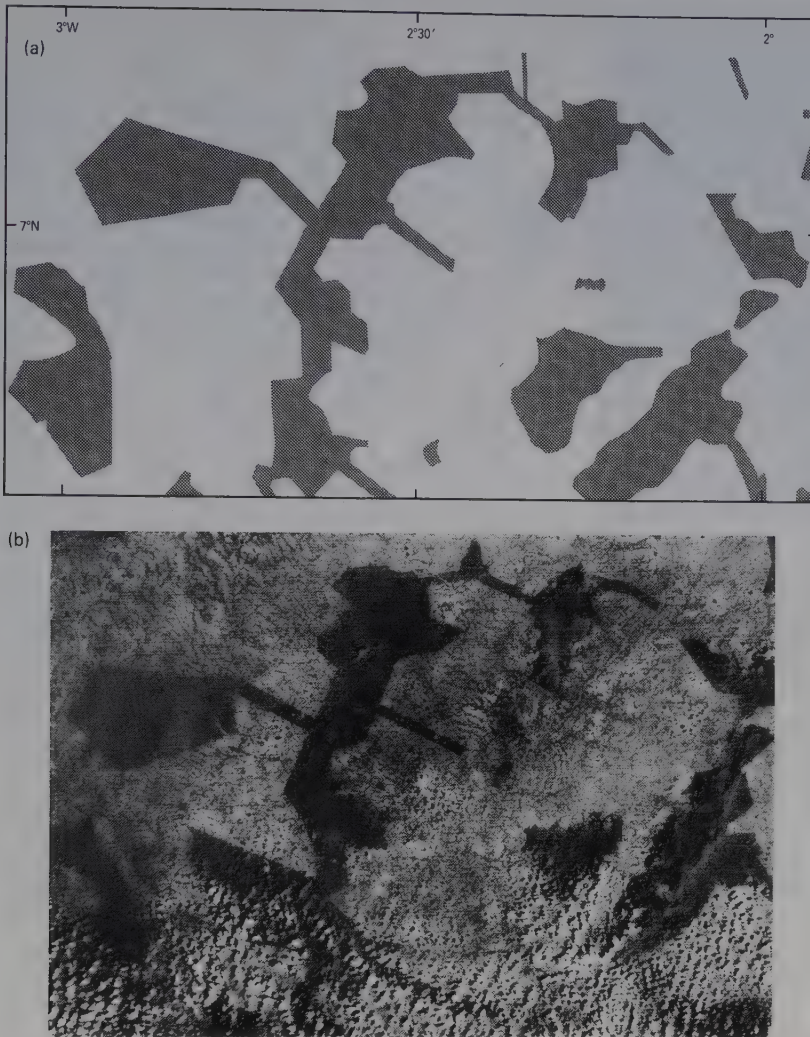
**Fig. 10.6.** Rain forest remnant patches in northwest Ghana. (a) Forest reserve map, 1955. (b) LANDSAT 2 image, 1973. Sunyani is just north of the scene. On the LANDSAT image the forests appear dark, like islands, in a pale-coloured sea of densely farmed land. Note that the shape and size of the reserves remained essentially the same over this 18 year period. This was despite heavy population pressure. The satellite scene was recorded at about 0930 and in the south small white clouds are casting dark shadows to their west.

trees growing deep in the jungle, such as durian (*Durio zibethinus*), in western Malesia,[241] should always alert one to possible past disturbance. The myth of the primeval forest dies hard, but although traditional societies had such an extensive impact on tropical rain forest, nowhere was it so devastating and irreversible as the impact of modern man, as described later in this chapter.

## 10.3. Minor forest products

Minor forest products, the term used for everything the forest provides in addition to timber, are a cornucopia of useful goods for mankind. Many are used only locally, a few enter international trade. Some were exploited formerly but have been eclipsed by factory products such as plastics.[242] Others still await discovery.

Forest Departments issue licences and collect royalties on minor forest products, though many are now obsolete. There are specific rates, for example, for leaves collected for food wrappers (Malaya: *Macaranga gigantea*), and for edible birds' nests (Borneo: produced by cave-dwelling swiftlets), and turtle eggs.
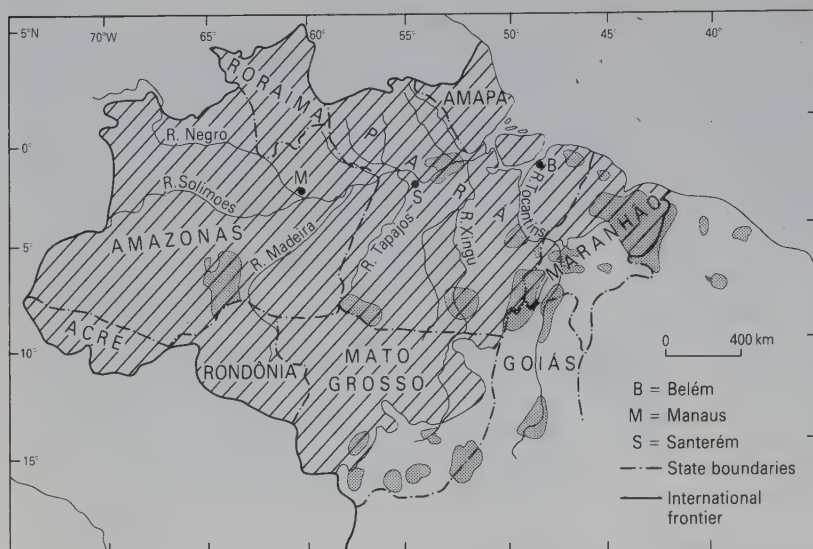
**Fig. 10.7.** Potential extent of the Amazonian rain forests in Brazil (Brown in Whitmore and Prance 1987, Fig. 2.4) with the main occurrences of the babassu palm (*Orbignya phalerata*) shown (Anderson *et al.* In Lugo *et al.* 1987). States, principal rivers, and cities shown.

Tropical rain forests contain many wild fruit trees, some of which are the ancestors and relatives of cultivated species, and many are species of medicinal importance or potential.[243] Furthermore, when fossil fuels are eventually depleted mankind is likely to make greater use of plants as sources of complex organic molecules, often as raw materials for manipulation. For example, the trunk of *Copaifera langsdorfii* (pau oleo) a leguminous tree of the Amazon produces an inflammable oil at a rate of 20 litres per 6 months, which is tapped and used locally instead of kerosene. Forests are a biochemical storehouse, scarcely yet exploited. Already edible protein can be extracted from leaves,[244] and lignin is utilized for the manufacture of plastics, ion-exchange resins, soil stabilizers, rubber reinforcers, fertilizers, vanillin, tanning agents, stabilizers for asphalt emulsions, and dispersants for oil-well drilling and for ceramic processing. Cellulose can be utilized for rayon and plastics and as a raw material for hydrolysis to sugar which, using yeasts, can be turned into alcohol and edible protein. Complex molecules such as steroids are conveniently obtained from plant sources. These so-called genetic resources are by no means yet fully known or exploited.

Crop plants that have developed major significance in international trade and whose origin is in rain forests are cocoa[245] and para rubber (*Theobroma cacao*, *Hevea brasiliensis*) from the neotropics; banana, citrus fruits, coconut,[246] and sugarcane (*Musa*, *Citrus*, *Cocos nucifera*, *Saccharum*) from the Eastern tropics, and oil palm (*Elaeis guineensis*) from Africa.

In addition, there are numerous fruits of regional importance, some now grown throughout the tropics (see Table 10.4, Fig. 10.8). Some of these species have scarcely altered from their forest ancestors. Others, for example *Durio zibethinus*, *Garcinia mangostana*, and *Carica papaya* (durian, mangosteen, and papaya), are unknown in the wild, as is the case of many of mankind's more important cultivated plants and domesticated animals too.

Rain forests provide innumerable species that are used locally in traditional medicine. Rather few have gained international importance. In this latter category, America is the source of a muscle relaxant used in major surgery, from roots of a climber (*Chondrodendron tomentosum*) which is one of the constituents of the arrow-poison curare, and of quinine (from the bark of *Cinchona*). Cocaine also originates from South America; it is prepared from the leaves of *Erythroxylum coca* (and was once introduced as a hedge plant to Asia but soon eliminated). Tubers of the yam (*Dioscorea*) are gathered from the wild in both America and Africa to provide diosgenin, the steroid used as the precursor molecule from which oral contraceptives and cortisone are made, though total synthesis is more common nowadays. Reserpine, a cardiac glycoside, which reduces high blood

## Table 10.4
### Rain forest fruits

| | |
|---|---|
| America: | *Annona muricata* (soursop) |
| | *A. reticulata* (bullock's heart) |
| | *A. squamosa* (sweetsop) |
| | *Bertholletia excelsa* (Brazil nut) |
| | *Brosimum alicastrum* |
| | *Carica papaya* and some relatives |
| | *Chrysophyllum cainito* (caimito) |
| | *Eugenia uniflora* (cayenne cherry) |
| | *Manilkara zapota* (sapodilla, and whose latex is also used for chicle, chewing gum) |
| | *Persea americana* (avocado) |
| | *Psidium cattleianum* (strawberry guava) |
| | *P. guajava* (guava) |
| | *Spondias mombin* |
| | *Theobroma grandiflora* |
| Africa: | *Afromomum melagueta* (grains of paradise) |
| | *Blighia sapida* (akee) |
| | *Canarium schweinfurthii* |
| | *Cola nitida* |
| | *Dacryodes klainiana* |
| | *Dialium guineense* |
| | *Hibiscus sabdariffa* (roselle) |
| | *Irvingia gabonensis* |
| | *Pentadesma butyracea* (tallow tree) |
| Orient: (mostly arillate) | *Artocarpus altilis* (breadfruit) |
| | *A. integer* (chempedak) |
| | *A. heterophyllus* (jackfruit) |
| | *Averrhoa carambola* (starfruit) |
| | *Durio zibethinus* (durian) |
| | *Eugenia aquea* (water apple) |
| | *E. jambos* (rose apple) |
| | *E. malaccensis* (Malay apple) |
| | *Garcinia mangostana* (mangosteen) |
| | *Lansium domesticum* (duku, langsat) |
| | *Mangifera* spp. (mango) |
| | *Nephelium lappaceum* (rambutan) |
| | *N. ramboutan-ake* (pulsan) |
| | *Salacca edulis* (salac) |
| | *Sandoricum koetjape* (sentul) |
| | *Shorea* spp. (illipe nuts, for a cocoa butter substitute) |
| Melanesia: (many nut trees) | *Barringtonia magnifica* |
| | *Canarium indicum* (ngali) |
| | *Pandanus* spp. |
| | *Pometia pinnata* |
| | *Terminalia* spp. |

This is a list of just some of the commoner regional fruits; several of them are now cultivated throughout the tropics.



**Fig. 10.8.** Limes, pupuña (peach palm) and cupuaçu fruits (*Citrus aurantifolia, Bactris gasipaes, Theobroma grandiflora*) on sale at a roadside stall, near Manaus, central Amazonian Brazil.

pressure and is also used in treatment of mental illness, is extracted from the roots of both African and Asian species of *Rauvolfia*, a shrub. The seeds of the Australian rain forest legume, the Moreton Bay chestnut (*Castanospermum australe*), have recently been discovered to contain a drug that might help combat AIDS. This illustrates the potential of tropical rain forests to meet new human requirements as they arise.

Then there are rattans, the stems of climbing palms, abundant throughout the Eastern tropics and the single most important rain forest product after timber (Fig. 10.9).

When you sit in a rattan chair at a rattan table on a rattan carpet with a rattan glass-holder, behind a rattan blind, with a rattan holdall, think of the hands through which the rattan came ....[247]

Rattans in international trade are currently worth *c.* £1500 million per year. One hundred and fifty thousand tons are traded annually. They come almost entirely from natural rain forest and have traditionally been one of the most important trade commodities for forest dwellers, passing through many middlemen to the great entrepôts of Ujung Pandang and Singapore. More recently social controls on their exploitation have broken

down.[248] Following the advent of logging roads and the consequent influx of people, rattans are now heavily over-exploited (Fig. 10.22c), and their trade is likely to collapse when the last virgin forests have gone, unless cultivation can be extended to meet the demand.[249]

## 10.4. Tropical rain forests today

Late twentieth century man, with his immense technological power, is out of harmony with nature and fast destroying it, too often holding the view that the planet was built only for people. There has been a progressive switch, especially in the decades since World War 2, in the way tropical rain forests are valued. Nowadays they are mainly regarded solely for their timber. Minor forest products have been largely forgotten. In 1938 the relative importance of timber and minor products traded from Indonesia was 55 to 45 per cent; today it is 95 to 5 per cent. Only part of the forest's goods have much importance in the contemporary world and little consideration is given to the services forests also provide and on which it is hard to put a cash value.[250]

### Rates of disappearance

Estimates made in 1980 of the rate at which tropical close forests and open woodlands were being altered by man are shown in Table 10.5. These data were collected by FAO and are the most reliable and comprehensive available. Tropical rain forests and tropical seasonal forests are lumped together as closed forests. This is because the national statistics from which the data are drawn do not distinguish the two kinds. FAO estimated that some twelve million hectares of closed forests are being altered per year. This figure includes forests totally destroyed by clearance, often after logging, $(7.5 \times 10^6$ ha), plus others logged for timber but left to regenerate $(4.4 \times 10^6$ ha). The important distinction between cleared forest and forest that is solely logged is not always made. It will be shown below that many of the functions for which forests need to be conserved are compatible with the kind of careful, limited timber extraction which was discussed in Chapter 7. The rate at which rain forests are being currently destroyed is causing their virtual disappearance from some places, for example Costa Rica, Sumatra,

and the Atlantic coast of Brazil (Figs. 10.10–10.12).

The estimated area of tropical moist forest is shown in Table 10.6 for 1975, and also the amount that the FAO report thought would be likely to remain at the end of the century. The decrease is due to land expected to be cleared of



**Fig. 10.9.** Rattans drying after treatment at a factory in Singapore.

These are the stout species rotan manau (*Calamus manan*), known in the trade as canes, and used for chair legs. Singapore was the main entrepôt through which rattans from all over the Malay archipelago were traded. Some were made into furniture, others were processed and exported to Hong Kong or Europe. Now producing nations have their own factories.

forest during the intervening period. The figures therefore show the global total tropical moist forest estate and its expected annual rate of depletion.

## Table 10.5
### *Rates estimated in 1980 of clearance and logging of tropical woody vegetation*

Estimate for 1981–85 (million ha year$^{-1}$)

1. Closed tropical forests
   | | | |
   |---|---|---|
   | cleared | 7.5 | a |
   | logged but not cleared | 4.4 | b |
   | hence altered (logged plus cleared) (a+b) | 11.9 | c |

2. Open woodlands
   | | | |
   |---|---|---|
   | cleared | 3.8 | d |

3. Forests plus woodlands
   | | |
   |---|---|
   | cleared (a+d) | 11.3 |

From Lanly (1982).
Data were collected by FAO and are the best available estimates but may be conservative if national reports to FAO were over optimistic. Moreover, the extensive fires in Borneo and Amazonia in the 1980s were not anticipated and certainly increase the figures. A repeat of the survey is due to be published in the early 1990s.

It can be seen in Table 10.6 that about half of the global moist forests are in South America. This is mainly the Amazon forests. The Zaire basin forests of Central Africa are the second most extensive. Note that there are big differences from place to place in the expected rate and amount of loss. Amazonia and Zaire will probably still have very extensive forests in AD 2000. By contrast West Africa, which had little moist forest in 1975, is expected to have lost half and the Eastern forests about one-fifth. Table 10.7 focuses more closely and shows the estimated rate of forest loss for particular countries in the early 1980s.

None of the estimates in Tables 10.5, 10.6 and 10.7 include the unprecedented and unexpected forest loss from huge fires which occurred after the data were collected. The rates of loss predicted have in fact been exceeded. The Great Fire of Borneo described on pp. 117–18 burned down some $4 \times 10^6$ ha of rain forest in 1983. It started by accident after an 18 month long drought. An even vaster area of rain forest has been deliberately destroyed by fire to create pastures on the southern fringe of the Amazon in Brazil, estimated from satellite imagery by INPE (the Space Agency of Brazil) to be $8 \times 10^6$ ha in 1987, another $8 \times 10^6$ ha in 1988, but somewhat less in 1989 which was rainier.[251] In each of 1987 and 1988 1.6 per cent of

## Table 10.6
### *Expected reduction in area of tropical moist forests, 1975–2000*

| | Area ($10^6$ ha) | | Annual loss | |
|---|---|---|---|---|
| | 1975 | 2000 | $10^6$ ha | As % 1975 area |
| Pantropical total | 1120 | 992 | 5.12 | 0.47% |
| of which main areas are: | | | | |
| **West Africa** | 14 | 7 | 0.28 | 2.0% |
| **Central Africa** | 170 | 166 | 0.16 | 0.09% |
| **Eastern islands**[a] | 172 | 149 | 0.92 | 0.53% |
| Asian continent | 119 | 94 | 1.00 | 0.84% |
| **South America** | 526 | 467 | 2.36 | 0.45% |
| Central America[b] | 101 | 93 | 0.32 | 0.3% |
| In the regions shown bold most of the moist forest is rain forest | | | | |

Data of FAO; Lanly and Clement (1979; Tables 1, 3)
[a] Malesia, Australia, Pacific islands
[b] Including Caribbean

Table 10.7

*Loss of rain forest 1980–85 in selected countries (World Resources 1986†)*

| | | Closed forest area 1980 (10³ ha) | Annual deforestation Area (10³ ha) | Per cent |
|---|---|---|---|---|
| **1. Large area deforested annually** | | | | |
| a) High rate of loss | | | | |
| America | Costa Rica | 1660 | 65 | 3.9 |
| East | Malaysia | 21300 | 255 | 1.2 |
| | Philippines | 12500 | 91 | 0.7 |
| Africa | Ivory Coast | 4910 | 290 | 5.9 |
| | Nigeria | 7560 | 300 | 4.0 |
| b) Low rate of loss | | | | |
| America | | | | |
| | Brazil[a] | 396000 | 1480 | 0.4 |
| | Peru | 70500 | 270 | 0.4 |
| | Venezuela | 33100 | 125 | 0.4 |
| East | Indonesia[b] | 123000 | 600 | 0.5 |
| | Papua New Guinea | 34400 | 22 | 0.1 |
| Africa | Cameroon | 18100 | 80 | 0.4 |
| | Zaire | 106000 | 182 | 0.2 |
| **2. Small area deforested annually** | | | | |
| a) High rate of loss | | | | |
| America | El Salvador | 155 | 5 | 3.2 |
| | Jamaica | 195 | 2 | 1.0 |
| East | Brunei | 325 | 7 | 2.2 |
| Africa | Guinea Bissau | 664 | 17 | 2.6 |
| b) Low rate of loss | | | | |
| America | Belize | 1390 | 9 | 0.6 |
| | Trinidad and Tobago | 368 | 1 | 0.3 |
| Africa | Central African Republic | 3590 | 5 | 0.1 |
| | Equatorial Guinea | 1290 | 3 | 0.2 |
| | Gabon | 20700 | 15 | 0.1 |
| | Sierra Leone | 798 | 6 | 0.8 |

3. Areas (10³ ha) for comparison

| France | 55000 | Tasmania | 6830 | Holland | 3620 |
|---|---|---|---|---|---|
| Wales | 2080 | New Jersey | 2030 | Rhode Island | 314 |

† Date are total national deforestation. Original source is FAO. The countries shown here are mostly rain forest. Figures rounded

[a] Partly Amazon rain forest, partly other kinds of forest; Hecht *et al.* (1988) give $1300 \times 10^3$ ha year$^{-1}$ for early 1980s Brazil Amazon deforestation rate

[b] No allowance for the 1983 Great Fire of Borneo which destroyed *c.* $3 \times 10^6$ ha in Kalimantan (pp. 117–18)

the South American tropical moist forest was burned down. The Amazon basin forests, which are still very extensive today, may be about to cross a threshold, faced by a whole series of threats to their integrity of which these fires are the most dramatic.

For the Amazon, as elsewhere, it is useful to distinguish the various causes of loss of rain

1940 (67%)    1950 (56%)    1961 (45%)

1977 (32%)    1983 (17%)

15°W

90°W
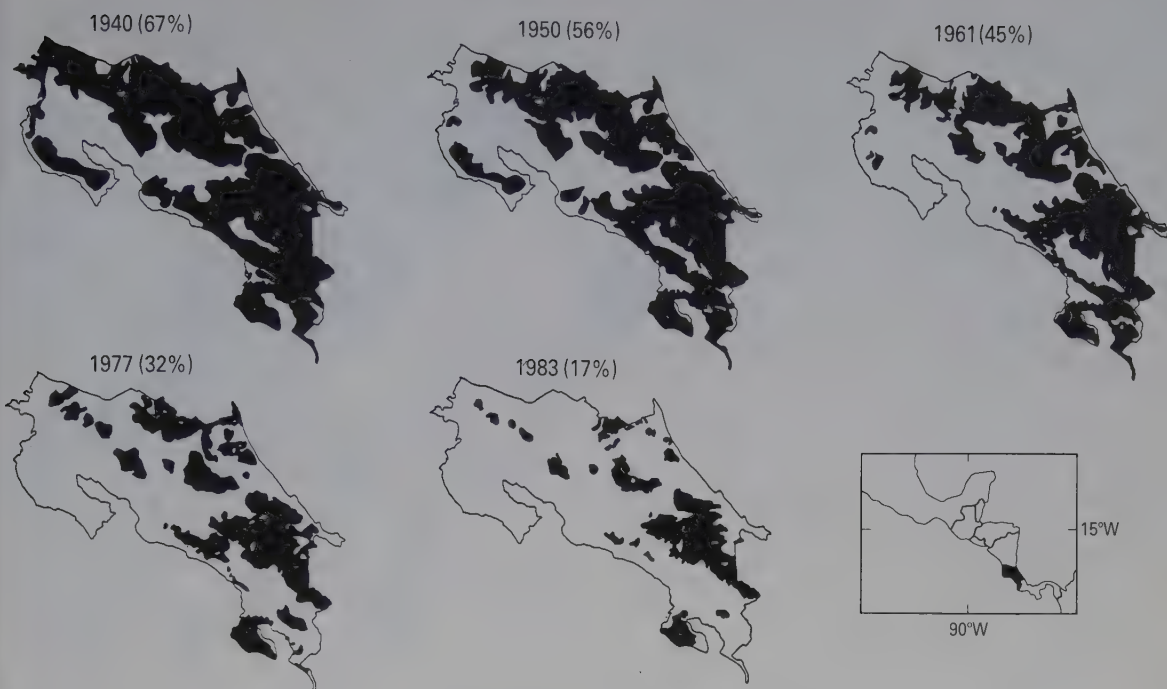
**Fig. 10.10.** Loss of primary forest, Costa Rica 1940–1983. (After Sader and Joyce 1988, Fig. 1.)

The forest formations ranged from rain forest to thorn forest in progressively drier climates. Note that besides primary forest (shown black) much degraded and regrowth forest also occurred, e.g. for 1983 the map shows the 17 per cent of primary forest cover but 33.5 per cent of the country had forest of some kind. By 1983 only rugged montane rain forests remained relatively undisturbed.

forests and to distinguish the various kinds and intensities of forest utilization. As with depletion rates there are important differences from place to place which are concealed by generalization. Let us now make this analysis and investigate the effect of these different kinds of human intervention on the forest.

**Forest conversion to other land usages**

*Agriculture.* This is the main purpose for which rain forests are cleared. There are several major kinds and their impact varies from place to place.

Conversion of tropical rain forests to pasture is especially widespread in the neotropics where there is a long tradition of cattle husbandry. The Atlantic Coast rain forests which once covered one million km$^2$ have been 99 per cent cleared, mainly over the past three decades (Fig. 10.12). Once roads were built, the larger trees were felled for charcoal to fuel iron smelters (Brazil had no in-

digenous fossil fuels) and pastoralists completed the destruction. Along with the plants, most of the animals of the Atlantic Coast forests have become endangered or extinct. This has been documented for the mammals and birds, but can only be surmised for most invertebrates. Very big pastures are also eating into the Amazonian rain forest massif, especially on its southern margin in Brazil. The figures quoted for the total pasture area vary widely, from 6 to 11 million ha in the early 1980s and will have increased since then (the area of Holland is 3 million ha).[252] Southeast Pará State has the most extensive pastures. A further *c.* $1 \times 10^5$ ha have been converted to pasture north of Manaus (Fig. 10.13) in order to provide meat for the city as a supplement to the river fish on which it was largely dependent. The rapid extension of the pastures is reflected in cattle numbers (Figure 10.14). These Brazilian pastures have been largely funded by fiscal incentives given by government in order to develop the region and

**Fig. 10.11.** Loss of primary forest, Sumatra, over about 5 years from 1980. Shown black is primary forest and forest that is logged but not substantially degraded. (Data of Whitmore 1984*b* and Laumonier *et al.* 1983, 1986*a*, *b*.)

Loss is principally in the lowlands and is mainly due to logging. Once logging roads gave access, spontaneous invasion occurred. There are also some big agricultural transmigration schemes.
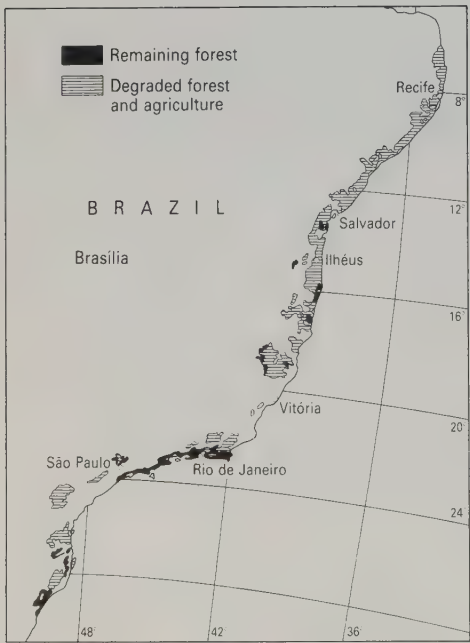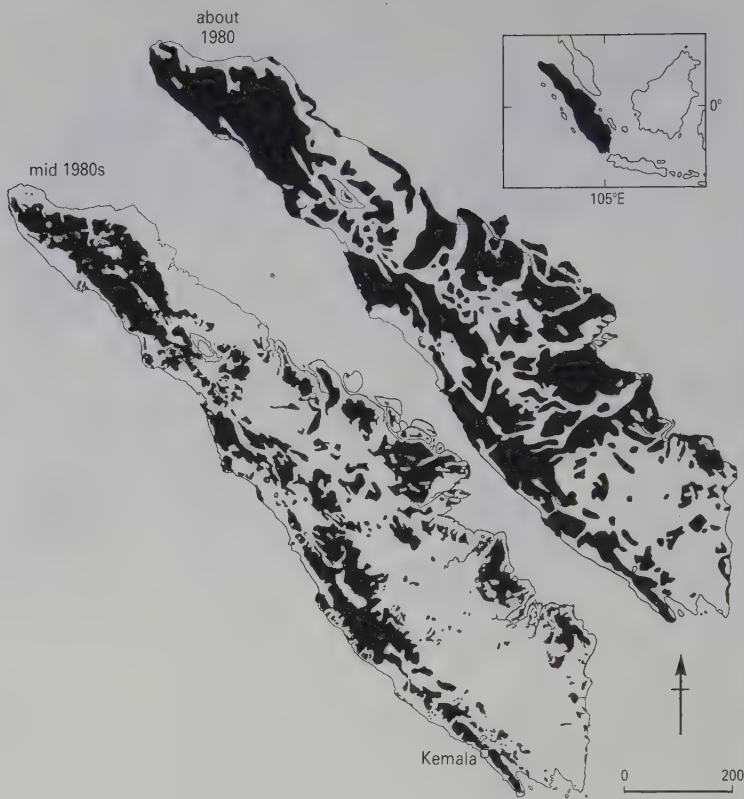


**Fig. 10.12.** The Atlantic coast rain forests of Brazil have very nearly disappeared. (After Prance and Campbell 1988, Fig. 8.)

In 1832 Charles Darwin had his first taste of the tropics at Salvador. These forests had a high percentage of endemics amongst both plants and animals.



**Fig. 10.13.** Cattle pasture north of Manaus, Brazilian Amazon. Primary lowland evergreen rain forest behind.
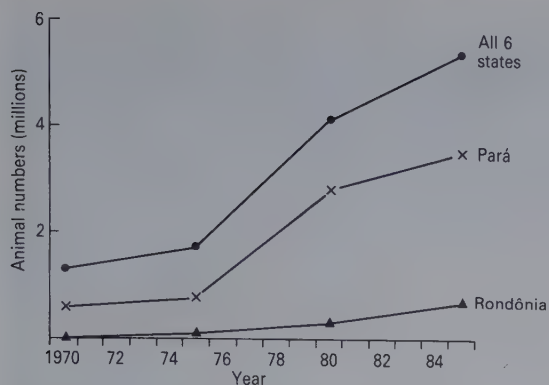
**Fig. 10.14.** Total cattle numbers in the Brazilian Amazon 1970–1985 and in the two states with the largest herds. (From Hecht *et al.* 1988).



**Fig. 10.15** Rain forest cover, Peninsular Malaysia. Estimates from various published sources. The final point is the proposed permanent forest estate for 1994. (After Aiken and Leigh 1988, Fig. 2.)

which make cattle ranching highly profitable. An economic simulation model has recently been constructed which demonstrates that, in the prevailing conditions of high currency inflation, 'improved' land increases in value sufficiently to make it profitable to create pasture even with no fiscal incentives or credit at all. Furthermore, pastures are used for under 10 years and then abandoned because, due to rising land values, it is profitable to shorten their life by overgrazing.[253] These reasons explain why livestock raising has continued to expand, and show how difficult it will be to arrest this cause of Amazonian deforestation. In Middle America pasture creation has substantially reduced rain forest cover. It is the main reason for forest attrition in Costa Rica, as shown on Fig. 10.10.[254]

Rain forests have also been felled and replaced by plantation tree crops, principally rubber and oil palm (*Hevea brasiliensis, Elaeis guineensis*) with cocoa (*Theobroma cacao*) taking third place. This form of conversion is having a major impact in Malaysia (Fig. 10.15), Indonesia, and Papua New Guinea. The crops are for export; they produce greater annual wealth than forest, of hard currency with which the nation can buy industrial goods. The plantations are sometimes run by large, often trans-national companies, sometimes by small-holders.

Plantations of trees grown for paper or for timber, which is in effect a kind of long-term agriculture, are becoming increasingly widespread and

important, as an alternative source of revenue as the virgin rain forests become depleted. Throughout the tropics *Gmelina arborea* (yemane; native to seasonal forests of continental southeast Asia) has grown well and is widely planted. In Sabah and the Philippines much *Paraserianthes (Albizia) falcataria* has been planted. Recently *Acacia mangium* (a pioneer tree of Queensland and adjacent Malesia) has gained popularity, partly because it shows a high rate of successful establishment even on very poor or dry soils. At Jari in the lower Amazon 74 447 ha of plantations had been established between 1970 and 1986, mainly *Gmelina* (23 per cent), *Eucalyptus deglupta* and *E. urophylla* (37 per cent), and *Pinus caribaea* (38 per cent) (Fig. 10.16).[255] Pines only thrive in seasonal tropical climates and have not been successful in perhumid climates.

Agriculture for food production, sometimes mixed with cash crops, has also made inroads into rain forest and has taken several forms. In Peninsular Malaysia urban squatters have been resettled by a quasi governmental agency, FELDA,[256] in big blocks of smallholdings, created out of lowland rain forest on flattish land. Jengka Triangle is the first and best known settlement; 70 000 people have been settled on 607 km$^2$ of former lowland rain forest. Indonesia, under its scheme of transmigration, has moved more than 4 million peasant

**Fig. 10.16**. Lowland semi-evergreen rain forest being cleared for tree plantations, the wood used to fuel a power station. Jari, Amazonian Brazil.

farmers, hundreds of thousands of persons annually, from densely populated Java, Madura, and Bali to other islands, commonly on to land carved out of the rain forest.[257] It is planned to increase the population of Irian Jaya by a third by the mid-1990s, to *c.* 2 million. However, the population of Java, Madura, and Bali increases by about 3 million annually. One consequence of transmigration in Indonesia is to bring together people with very different cultural backgrounds.

Brazil in the 1960s and early 1970s built several strategic roads through the Amazon forests and moved peasant farmers to smallholdings along them from the overcrowded arid northeast, notably along the Trans-Amazonica highway. The slogan was 'a land without men for men without land'. The result is that today there are strips of farming stretching part-way across southern Amazonia. The Andean nations west of the Amazon have also built roads down into the forest (Fig. 10.17).

The final mode of agriculture may be called unplanned, because government plays no direct role and it is usually illegal. This is the felling of rain forest and subsequent settlement by landhungry peasants. The unsustainable kind of shifting agriculture these people often practise, and its impacts on the western Andean fringe of Amazonia, were mentioned on p. 135. Roads built for access by logging companies often provide the arteries along which such invasion of the forest occurs. For example, Buginese from Sulawesi moved westwards across the Makassar Strait into east Kalimantan and set up farms, with pepper as a cash crop, in previously uninhabited dipterocarp forests, once logging roads gave access.[258] The intention of the Indonesian government had been to make these forests part of the permanent forest estate to provide a continual source of timber. In the Philippines many production forests have been similarly invaded and destroyed. There, by
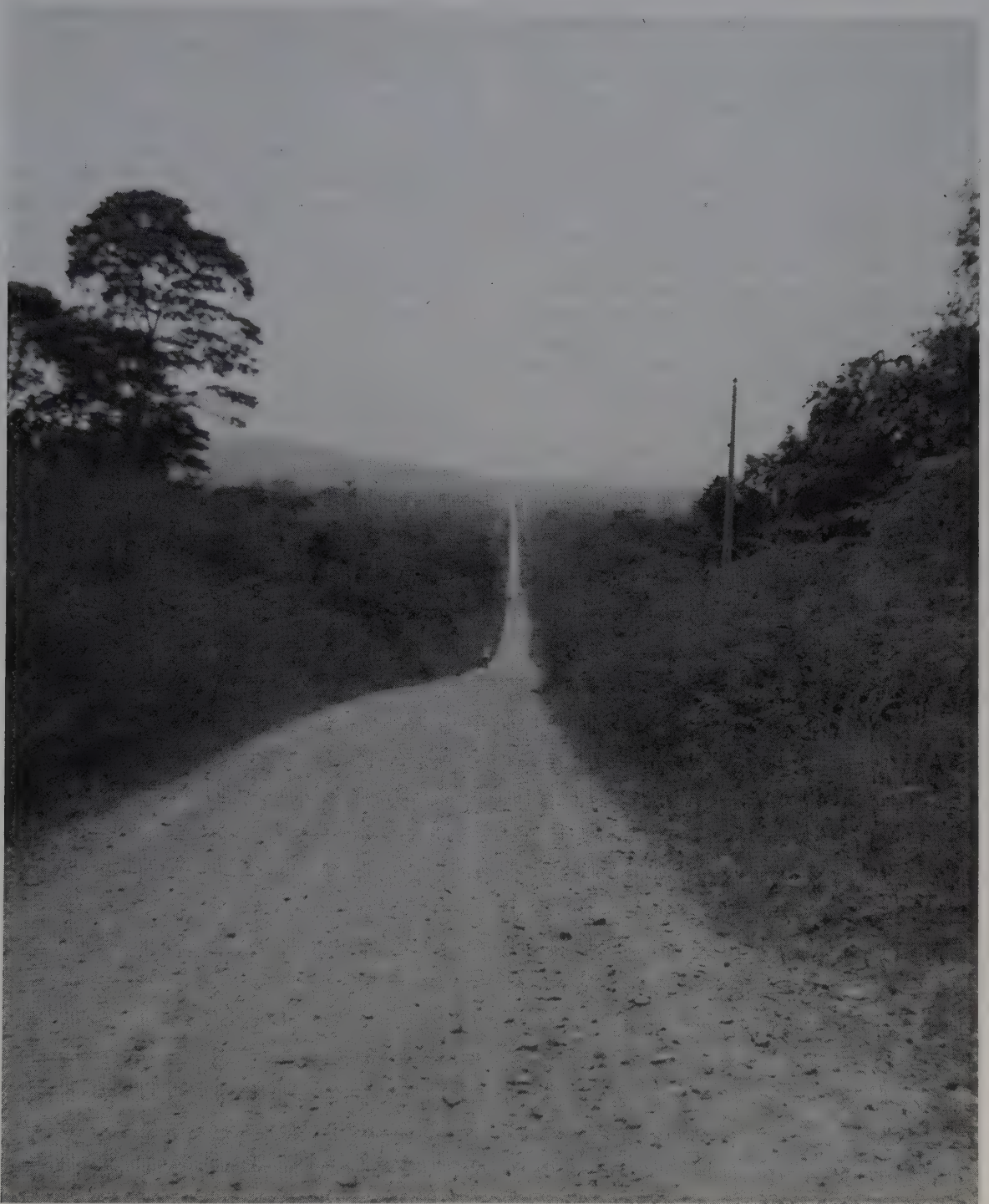
**Fig. 10.17.** Access road for oil exploration built from the base of the Andes into the Amazonian rain forest, Ecuador.

Throughout the humid tropics farmers and hunters quickly penetrate previously inaccessible rain forests as soon as such roads are built.

1986, an estimated million people were living on forest land, double the number in 1979 (Fig. 10.22d).[259] In Nigeria, peasant farmers have now nearly totally destroyed the rain forest: less than 10 per cent remains.

A road, the BR-364, funded by the World Bank, was built into Rondônia State in southwest Amazonian Brazil during the 1970s. It was planned to move in farmers to settle the better soils. In fact, landless peasants invaded from southern Brazil and overran the region. Population increased from 10 000 in 1960 to over a million by 1985. Forest loss accelerated from $1.2 \times 10^5$ ha in 1975 to $16 \times 10^5$ ha in 1985 (Fig. 10.18). Parts of the land were so infertile that agriculture soon failed and a low scrub replaced what had been pristine high forests populated at a low, sustainable density by Amerindians only a few years before. In the 1980s this road was extended westwards into Acre State.[260] The tappers of wild rubber in Acre united in opposition to the felling of their forests for pasture and were harassed by certain of the developers. Many hundreds of tappers were murdered including in late 1988 their spokesman. The outside world at last awoke to what was happening and stood aghast. This sad episode certainly increased international sensitivity to the progressive rape of Amazonia.

Pressure of increasing population drives all these human migrations. Increasing population leads also to an increase in the area under the sustainable kind of shifting agriculture. It too breaks down when expansion is no longer possible and increasing population forces cultivation beyond the carrying capacity of the site (section 8.1).

Shifting agriculture in its multifarious forms was identified as the single most important reason for loss of tropical forests by FAO, in their analysis summarized in Tables 10.5 and 10.6. In the early 1980s it was estimated to be responsible for 35 per cent of all New World deforestation (with conversion to pasture second), and in Africa and Asia 70 per cent and 49 per cent respectively.[261]

*Dams.*   The Tocantins river, a major southern tributary of the lower Amazon, has had one hydroelectric dam constructed south of Tucuruí which has flooded 216 000 ha. Six more dams are planned.
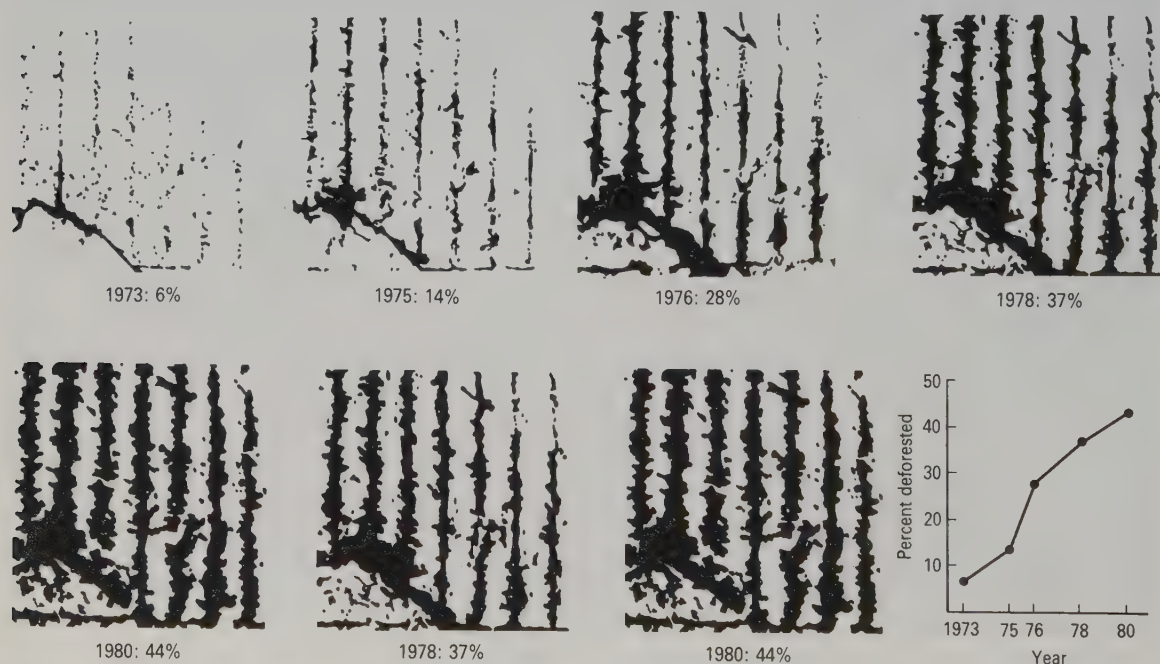


**Fig. 10.18.** Progressive clearance (shown black) of forest for farms in southwest Amazonia 1973–1980 along roads 5 km apart. The main national highway, BR-364 is in the southwest. The area is the quarter degree square whose northwest corner lies at 11°15′S, 61°30′W. (Fearnside 1986, Fig. 5.)

The World Bank has provided funds. Other south bank tributaries have further suitable sites.[262] The location is where these northwards flowing rivers run as cataracts down off the hard rocks of the Brazilian shield on to the great Tertiary central Amazonian sedimentary plain. Dams cause riparian forests and the whole aquatic ecosystem to be engulfed. Amerindians and other rural people who live mainly along the rivers have their homelands and societies destroyed.

In Sarawak one hydroelectric dam has been built and a second is proposed. The Batang Ai dam flooded 8700 ha and displaced 3000 traditional shifting cultivators from 33 longhouses. The loss of their ancestral lands forced them into cultivation of cash crops on the 4.6 ha per family given in compensation. The proposed Bakun dam would flood 73 000 ha, an area larger than Singapore, and displace 5000 people. Both schemes destroy the traditional societies which are displaced.[263]

*Mines.* These are also totally destructive of rain forest, but usually only on a small area. Even where there are laws to restore forest cover, mining may lead to forest disruption over a wide area. An example is Carajas in southeastern Amazonian Brazil.[264] Here, vast rich deposits of iron ore and other minerals have been exploited since the mid-1980s. The mine itself is to be reforested but the Greater Carajas project involves massive development of a large region centred on a 900 km railway built to the Atlantic coast. The ores are largely exported to Europe, and the scheme has received substantial funds from both the European Community and the World Bank. Some of the iron ore is smelted at furnaces situated along the railway, using charcoal made out of rain forest trees.[265] It is planned eventually to produce charcoal from vast *Eucalyptus* plantations. Based on yields of eucalypts at the Jari plantations further north 700 000 ha will be needed, seven times the area at Jari. However, because of the high cost and technical difficulties of establishing plantations, charcoal is likely to come from the natural forest for as long as any exists. Felling for charcoal and for agriculture is currently extirpating a broad corridor of forest along the railway together with the livelihood of the people who inhabited it.

## Forest utilization

Replacement of forests by agriculture totally destroys them. By contrast, their use for wood production can leave them more or less intact, depending on the mode and intensity of utilization (Figs. 7.21–23, 10.19, 10.20).

It is conventional to divide wood utilization into fuelwood, which includes charcoal, and other uses, so-called industrial wood. Table 10.8 shows global annual wood use and its various components. About half of global use is as fuelwood of which two-thirds is from tropical broadleaf species (i.e. hardwoods).[266] This reflects the importance of domestic fuel in the tropics, and, because the greatest populations are in the seasonal tropics, the main source is tropical seasonal forests.[267] Industrial wood is supplied 70 per cent by conifers which are pre-eminent for paper manufacture, and provide the main constructional timber of the industrialized northern nations. Only 11 per cent of total annual use of industrial wood is supplied from the tropics, and this mainly comes from tropical rain forests, not seasonal forests.[268]

### Table 10.8
*World wood utilization (million m³)*

| 1. Utilisation by end use | | | |
|---|---|---|---|
| Total utilization (1987) | | 3350 | |
| of which industrial wood | | 1630 | (49%) |
| fuelwood | | 1720 | (51%) |

| 2. Utilization by timber class and source | | | |
|---|---|---|---|

| | Conifer (softwood) | Broadleaf (hardwood) | | |
|---|---|---|---|---|
| | | total | tropical | temperate |
| Industrial wood | 70% | 30% | 11% | 19% |
| Fuelwood | 16% | 84% | 65% | 19% |

Data from Pringle (1976) and FAO (1989)

*Timber production.* The exploitation of rain forests has progressively increased (Fig. 10.21). Southeast Asia has become the dominant source.[269] West Africa has become less and less important and in places is running out of forest. For example, Nigeria is now a net importer of

**Fig. 10.19.** Lowland evergreen rain forest on Vanikolo, Santa Cruz Islands, Melanesia, 8 months after the timber (mainly *Agathis macrophylla*, Fig. 10.20) was extracted. Note regrowth of the big-leaved pioneer *Macaranga aleuritoides* on the right. The climate is extremely wet, hence the abundance of climbers and epiphytes.

Logging destroyed all the virgin stands (and source of seed) of *Agathis* but there was vigorous regeneration from seedlings. No silvicultural system was in operation. This was a 'cut and clear-out' operation, and could loosely be referred to as a clear-felling for *Agathis*, but as can be seen the matrix of the forest survived except along tracks as in the centre of this photograph. Clear felling of tropical rain forest for timber has a quite different result from clear felling in Europe or North America because much less is removed. Where, as here, the term is loosely applied to a monocyclic felling operation, it has misleading connotations which can cause confusion for the tyro.

**Fig. 10.20.** *Agathis macrophylla*, Vanikolo kauri, a valuable timber species which at maturity develops a heavy sympodial crown. Note the pioneer regrowth of *Macaranga tanarius*. Vanikolo, Santa Cruz islands.

timber and, with Ivory Coast, faces total disappearance of its rain forest. The dipterocarp forests of the Philippines, then of Malaysia and, since the early 1970s, of western Indonesia (see the sudden rise on Fig. 10.21) have been the main Asian source. Part of the cut has come from land being cleared for other uses, the rest from areas designated as forest reserves. Peninsular Malaysia has very little loggable lowland virgin

forests left, nor does the Philippines (Fig. 10.22b),[270] where annual timber production is already declining steeply (Fig. 10.22a). The other virgin dipterocarp forests of western Malesia are unlikely to last beyond the year 2000. The second cut of these forests will yield a lower volume per hectare, and very little where over-exploitation took place first time.

Forests are a potentially renewable source of timber, which is in this respect unique amongst industrial raw materials. Unfortunately sustainable production has in most places been jeopardized by careless and excessively heavy exploitation. In addition, as discussed above, logging roads give access to settlers who destroy the forest, or to hunters who kill many of the animals and so disrupt ecosystem functioning.

One reason why dipterocarp timbers have such a strong international market is because they can be grouped for sale into just a few classes (Table 10.9). Thus, even though the southeast Asian dipterocarp rain forests are very diverse and rich in species, a steady supply of a few grades of timber is maintained and this suits the users. An attempt to boost the sale of West African timbers by grouping them largely failed because the properties of the individual species were too diverse.

The Amazon forests are a huge, little exploited timber resource, so far playing a relatively minor role in international trade; (Fig. 10.21). Many Amazonian species have heavy, dark, siliceous timber (Table 10.10) which does not meet modern requirements, and they have proved impossible to group into end-use classes (Table 10.9), with the result that continuity of supply cannot be assured and a big international market cannot be developed (Table 10.11). Amazon timbers will be no substitute for those from southeast Asia. They are
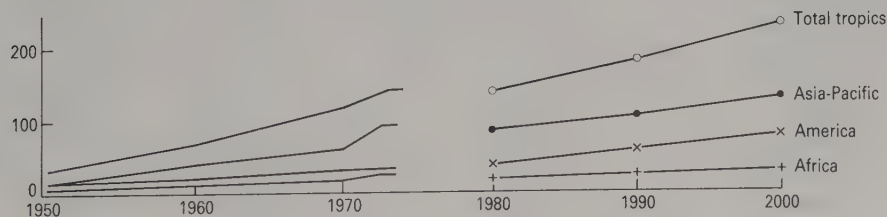


**Fig. 10.21.** Actual and estimated tropical hardwood production, 1950–2000. (1950–1973 after Pringle 1976; 1980–2000 estimated by FAO 1982.)

Table 10.9

*Grouping of tree species into timber classes and their share of total log production*

| | Number of species | % total log production | Production[a] $(m^3 \times 10^{-5})$ |
|---|---|---|---|
| Southeast Asia[b] | | | |
| top 5 classes | 195 | 59 | 390 |
| (of which meranti[c]) | (95) | (27) | (180) |
| top 10 classes | 229 | 73 | 490 |
| Africa | | | |
| top 5 classes | 7 | 45 | 55 |
| (of which obeche[d]) | (1) | (16) | (20) |
| top 10 classes | 13 | 59 | 72 |
| South America | | | |
| top 5 classes | 13 | 40 | 28 |
| (of which *Virola*) | (7) | (24) | (17) |
| top 10 classes | 13 | 50 | 35 |

From Erfurth and Rusche (1978, Table 4)

[a] In 1973

[b] A few species occur in more than one class

[c] Mostly *Shorea*, a few *Parashorea*

[d] *Triplochiton scleroxylon*

Only in Southeast Asia can numerous species be sold together as a few timber groups and that region has far higher production

Table 10.10

*Timber density classes in Pará State, Brazilian Amazonia, amongst trees over 0.25 m in diameter and with over 2 m³ timber per hectare*

| Region (area and % sampled) | Volume $(m^3\ ha^{-1})$ | Timber density class (%) | | |
|---|---|---|---|---|
| | | Light (<0.5) | Medium (0.5–0.7) | Heavy (⩾0.7) |
| Xingu-Tocantins (1.7 million ha, 0.01%) | | | | |
| Caxuana | 192 | 5 | 21 | 74 |
| Portel | 141 | 0 | 16 | 84 |
| Cameta West | 129 | 4 | 18 | 78 |
| Tocantins-Guama/Capim (3.1 million ha, 0.01%) | | | | |
| Acara | 140 | 2 | 16 | 82 |
| Belem-Sul | 137 | 2 | 16 | 82 |
| Rio Capim | 130 | 2 | 12 | 86 |
| Tapajos-Xingu (1.5 million ha, 0.03%) | | | | |
| Planalto I | 164 | 0 | 53 | 47 |
| Flanco I | 100 | 0 | 32 | 68 |
| Flanco II | 175 | 0 | 40 | 60 |
| Planalto II | 160 | 0 | 29 | 71 |
| Planalto III | 69 | 3 | 52 | 45 |
| Flanco III | 92 | 0 | 20 | 80 |

From Whitmore and Silva (1990)

Table 10.11

*Utilization of different density classes of timber in South America in 1971/3*

| Wood class | Density (g cm$^{-3}$) | Production per cent | Export per cent |
|---|---|---|---|
| Low density | <0.5 | 14 | 4 |
| Medium density | 0.5–0.65 | 53 | 65 |
| Upper density | 0.65–0.8 | 7 | 3 |
| High density | >0.8 | 10 | 5 |

From Erfurth and Rusche (1978)

Low and medium density timbers dominate production and export. In many South American forests, however, trees with upper and high density timber dominate

mostly suitable only for special uses, high-cost, low-volume goods such as musical instruments, and not for plywood, peeled veneers, or light construction. Particle board could be produced but would be extremely heavy and therefore of limited use. A recent development, however, is of a big internal market, for example within Brazil.[270a] The share of Amazonian timbers in the national annual wood harvest increased there from 14 to 44 per cent in the decade 1976–1986, extracted from dry land forests made accessible by newly built roads. Now, from Paragominas municipality in northern Pará State, for every beef truck leaving for southern Brazil, dozens
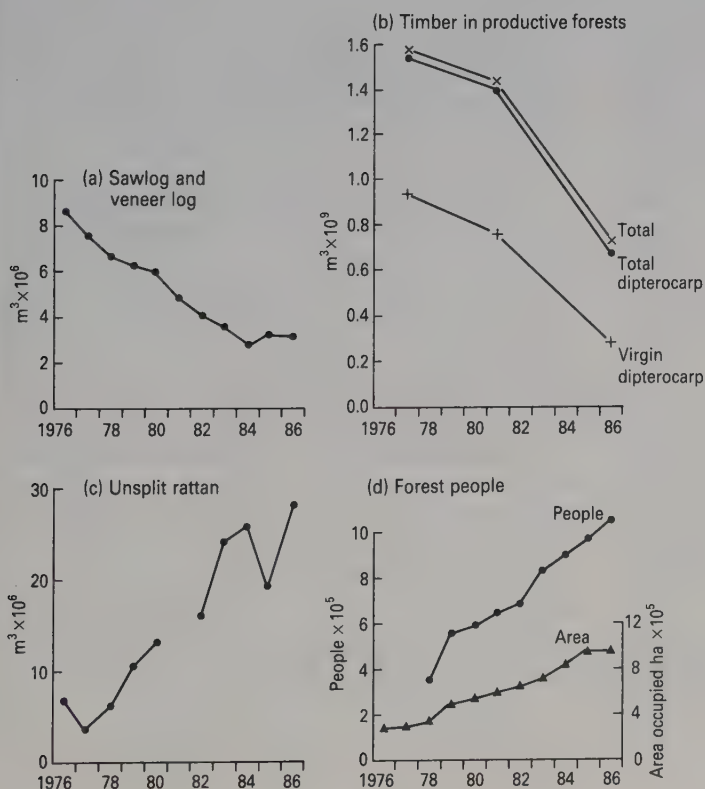


Fig. 10.22. A decade of decline of the Philippine rain forests, 1976–1986. (From Philippines Bureau of Forest Development Forestry Statistics.)

Annual log production (a) dropped to one-third as the accessible forests were logged. Despite this reduction the annual cut far exceeded growth and the remaining timber volume (b) was reduced to one-third. Rattan production (c) increased six-fold (to an unsustainable rate) and people living on forest land (d) multiplied threefold.

beef truck leaving for southern Brazil, dozens more leave carrying wood. Residual trees are in future likely to be felled for charcoal, with the Carajas-San Luis iron ore railway only 200 km distant. The first charcoal for the smelters built along this railway left Paragominas late in 1988.

Light hardwoods form only a low percentage of many Amazonian forests. In particular *Swietenia macrophylla*, mahogany, is absent from the central part of the basin, occurring solely in a broad, irregular southern belt. Amazonian mahogany[271] has entered international trade since the strategic roads were built in the early 1970s. The pastures of Pará State occur partly within the mahogany belt, and many fenceposts and farm gates there are built from it.

*Chips.* A more intensive utilization of rain forest than as a timber resource is the production of wood chips. The three dry land rain forest chip operations were mentioned in section 8.3. In addition, wood chips are obtained from some Asian mangrove forests and used in Japan as the raw material for rayon.

*Fuelwood.* Production from rain forests has until recently been relatively unimportant, with the notable exception of the virtual destruction of the Brazil Atlantic Coast rain forests for industrial charcoal.[272] There are major plans for the Amazon forests which have been described above: fuelwood for power stations and to produce charcoal for iron-smelting along the Carajas railway, which has already commenced.

## Animals in logged forest

Research by A. D. Johns at three locations in lowland rain forest, at Sungei Tekam in the Jengka area of Malaya,[273] at the Danum valley, Sabah, and near Tefé, Brazil has shown that at those forests bird and mammal populations were surprisingly robust in the face of a single logging operation.

At Sungei Tekam logging occurred on part of a big area of forest. This forest contained 223 species of birds, of which 23 per cent occupied tall

primary forest. Of 56 'large' mammal species 9 per cent occurred exclusively in primary forest. Most of the birds were still found after logging, but at low population densities. Only a few species, highly specialized insectivores and cuckoos, were missing, and these too had returned within 12 years after logging. The canopy-dwelling primates and squirrels all returned soon after logging. The Danum survey took place in an isolated block of forest which was totally logged. It showed that animals found after logging are not immigrants from elsewhere but are indeed the original population.

These studies indicated that many animal species are adaptable to the changed conditions of logged forest. During logging the animals retreat to pockets that remain untouched, and keep quiet (no calling is heard). The restocking of the forest after logging is not by immigrants from outside but from these animals moving out of the pockets. At Sungei Tekam primates ceased to breed during the logging period, as one year's births were absent when the forest was recensused. The data suggest that species utilizing patchy food resources are pre-adapted to survive logging, unless their resources are reduced too far. Furthermore, terrestrial browsing species, such as deer, elephant, and tapir, prefer to feed in logged forest because of the greater abundance of browse near the ground.

Longer-term monitoring is needed, especially to investigate the influence of further logging, which on a polycyclic system could occur as soon as after 20 years. Repeat logging on such a short cycle is very likely to eliminate the pockets of primary forest which provided the refuges at the first logging and to be too frequent to allow complete recovery of all the animal species. So, although Johns's research gives grounds for some optimism, in fact the long-term prognosis for species survival in repeatedly logged production forest is not good. Moreover, the lesson of the Great Fire of Borneo of 1983 was that logged forest is prone to fire in the rare droughts which occur once every few decades (p. 117), and such fires do serious damage to the ecosystem, including its animals.

## 10.5. Causes for concern

There is widespread concern about present-day human interference with tropical rain forests. We have just shown that interference takes many forms and that these vary from place to place, with pantropical generalizations concealing important differences. The consequences of modern tampering with the forest are also diverse. They fall into three main groups, effects on climate, on biodiversity, and on human societies. Let us consider the consequences of the various human impacts in order to see to what extent the concern is justified.

**Climatic change**

One issue on which discussion of rain forest destruction focuses is the changes that might occur to local, regional, or global climate. This is an immensely complicated subject, and it is beyond the scope of the present book to discuss it in full. The experts are not in full agreement but knowledge is improving all the time. Vegetation can affect climate in several different ways, via heat balance, surface roughness, the hydrological cycle (precipitation and evapotranspiration), and the production of various gases, notably carbon dioxide.

*Heat balance.* Forests look dark on aerial photographs (Fig. 10.7). This is because they absorb more of the incident solar radiation than other vegetation types, in other words their albedo is low. It has sometimes been suggested that des-

truction of forest will have dramatic effects on regional or global climate. The argument is that any replacement vegetation has a higher albedo because it absorbs less of the incident radiation, and that this alters the regional heat balance and hence the climate. The argument hinges, however, on how much the albedo differs between forest, cultivated crops, and bare land. It can be seen in Table 10.12 that, in fact, all vegetation has a fairly low albedo compared to bare earth. In reality tropical forest is either replaced by agriculture, often as tree crops, or by regrowth forest or scrubland. Nature abhors a vacuum and nowhere more so than in the humid tropics, where bare earth is revegetated within a matter of weeks or months. It follows that the effect on climate by a change to the albedo of parts of the humid tropics may not be very large.

The more heat that is absorbed the more there is available for evapotranspiration of water and to create air convection currents, so albedo by these mechanisms also influences the hydrological cycle.

*Surface roughness.* Forest canopies have an uneven upper canopy surface, most marked in lowland tropical rain forest with its scattered emergent trees. Tree plantations and tree crops are also fairly rough compared to pasture. Surface roughness of vegetation affects climate by its influence on air currents and by the increased evapotranspiration which occurs as a result of turbulent mixing at a rough surface.

Table 10.12
*Some climatic properties of different surface covers*

| | Forest | Grass | Herbaceous Crops | Bare |
|---|---|---|---|---|
| Potential evapotranspiration[a] (mm year) | 850 | 550–750 | 550–750 | 400–500 |
| Surface albedo[b,c] | 0.12 | 0.16–0.2 | 0.2 | 0.35 |

[a] Baumgartner and Kirchner (1980) in Henderson Sellers (1980)
[b] Dickinson and Henderson Sellers (1988)
[c] Potter *et al.* (1981)

*Hydrological cycle.* Vegetation evaporates and transpires much of the rainfall it receives and this water vapour forms clouds which fall as further rain. All vegetation has high evapotranspiration compared to bare land (Table 10.12) and in particular primary forest, logged forest, secondary forest, and tree plantations (oil palm, rubber: *Elaeis guineensis, Hevea brasiliensis*; plus timber species) have fairly high evapotranspiration rates; this is partly because of the albedo and surface roughness effects described above.

Several studies have been made in the tropics to compare the water yield in the drainage streams of paired, adjacent catchments with different vegetation cover and each of a few square kilometres in area.[274] In general the water yield increases if tree cover is removed because evapotranspiration diminishes. These studies also demonstrate that the ability to absorb periodic rainfall into the soil and release it into streams in a steady flow (sometimes referred to as the 'sponge effect') is not unique to forests, but also occurs in grassland so long as there is a sufficient volume of roots to maintain soil porosity. But where, as is usually the case, a catchment has rock outcrops, bare earth, roads, or buildings its sponge effect is reduced and outflow may become very uneven.[275] Some reduction in the sponge effect is very likely to occur following agricultural development or where a forest is dissected by logging tracks and compacted areas.

There are two cases where tropical rain forest cover probably does have a direct effect on the amount of precipitation.[276] One is that upper montane forests (which occur above the level of prevalent cloud formation; section 8.5) physically strip water from the fog which frequently pervades the canopy. In the wet season this so-called occult precipitation is about 7–18 per cent of rainfall but it may reach over 100 per cent during the dry season. If upper montane forest is removed water entering the ecosystem is reduced. The second case is the Amazon. This vast forest receives its rain from the northeast trade winds blowing in from the Atlantic Ocean; rain falls; much water is evapotranspired, re-enters the atmosphere, is blown towards the Andes, and falls again as further rain. Measurement of the heavy isotopes of oxygen and hydrogen $^{18}O$ and D (deuterium) which are less evapotranspired, shows

that inland Amazonia appears to receive about half of its rainfall from recycled water.[277] Were big parts of the Amazon rain forests to be replaced by vegetation with lower evapotranspiration, there would be less water recycling and inland rainfall and river flow would be reduced. The result of reduced rainfall would probably be a longer dry season. At Manaus there are already 73 dry days per year and it is drier still in the lower Amazon (Fig. 2.1). Another consequence of lower evapotranspiration would be to reduce cloud, so the climate would become sunnier. Rain forests in parts of Amazonia might already be metastable, existing near a threshold, and might not persist if the climate became much more seasonal and sunny than it is today.

Computer models have been used several times to investigate the changes to regional climate that would result from altering the Amazon basin from broadleaf evergreen forest to scrub grassland. These models have become progressively more sophisticated to include more variables. The most recent simulation[278] allows for several major changes following deforestation. These include reduction in evapotranspiration and increase in albedo as described above. They also include reduction in soil depth, in vegetation cover, and in surface roughness, as well as increases in surface runoff and root density. When the model was run for 13 months from moment of deforestation the main results were to decrease both rainfall interception and total evapotranspiration. The consequences were an increase in runoff and a rise of 1–3 °C in air temperature and of 2–5 °C in soil surface temperature (because of reduced latent heat of evaporation). No inferences were possible concerning changes to regional or global climate, for which the modelling problems are fiendish. These alterations to the climate of the Amazon basin would be detrimental to any remaining forest, which, as mentioned above, may already be existing near a threshold.

*'Greenhouse' gases.* Global climate is becoming warmer because certain gases are increasing in concentration in the atmosphere.[279] These gases act like the glass of a greenhouse by preventing the radiation back to space of infra-red radiation. The main gas is carbon dioxide and this creates

about half the greenhouse effect. The other half is made up mainly of the naturally occurring gases methane and oxides of nitrogen ($NO_x$).[280] Most greenhouse gases come from burning fossil fuel, partly in internal combustion engines (which contributes $NO_x$ as well as $Co_2$).[281] The destruction of tropical forests, if coupled with burning, adds $CO_2$ and $NO_x$, but replacement forest fixes $CO_2$ again. Oxidation of soil humus, which occurs after the forest is removed, adds more $CO_2$. Cattle produce *c.* 300 l methane each per day by bacterial fermentation in the rumen[282] and cattle numbers are increasing as pasture replaces rain forest, especially in the neotropics. An important sink which removes perhaps large amounts of $CO_2$ from the atmosphere is the phytoplankton which live in the surface waters of many oceans and which incorporate $CO_2$ both in organic matter by photosynthesis and in their calcareous cell walls. Some $CO_2$ also dissolves in the oceans as bicarbonate and the magnitude of this buffering effect is difficult to calculate.

The greenhouse warming effect works the opposite way from the albedo cooling effect of tropical forest destruction. Overall, the contribution to global climatic change made by the alteration and destruction of tropical forests is very difficult to quantify. Major difficulties in the climatic models are how to allow for the extent and reflectivity of different kinds of cloud, because these have different influences on the heat balance.[283]

A tract of rain forest in the climax, virgin state is in dynamic equilibrium. For example areas in the building phase of the forest growth cycle, where biomass is increasing (Fig. 7.31), are balanced by areas that are down-grading. Biomass is created by photosynthesis, whereby carbon dioxide is reduced and oxygen is released. Later, when the patch of forest falls and decomposes the process is reversed.[284] Thus, virgin forest is in a state of balance. Overall it is neither adding nor removing either carbon dioxide or oxygen.

## Loss of biodiversity

Unlike essentially all other scientific disciplines conservation biology is a science with a time limit, with the clock ticking faster as the human population continues to increase[285]

Biodiversity became a buzzword of the late 1980s. Reduction in structural diversity inevitably follows from human interaction with tropical rain forests as they are progressively simplified by increasing degrees of interference, for example for timber utilization. Species numbers of both plants and animals are also usually reduced. Where destruction is total, by conversion of the forest to agriculture, extinctions probably occur because all rain forests contain local endemics of limited geographical range and because for animals their habitat has been destroyed. Reduction within species of either the numbers of individuals or of geographical range is a more insidious loss of biodiversity, sometimes evocatively called 'genetic erosion' because of the likely loss of ecotypes and other genetic variants.[286]

The debate on the consequences of the loss of tropical forests sometimes includes spectacular figures for numbers of species currently becoming extinct, several per day. Such figures are highly speculative[287] and are mostly of unknown and undescribed insects (cf. p. 58). Documentation of extinctions, or of species becoming endangered, are sufficiently serious without such journalistic hyperbole. For example, were the American rain forests to be reduced to half their original extent by the end of the century, reasoned calculation predicts the loss of 13 600 plant species, or 15 per cent, and 12 per cent of the bird species.[288] Already in the decade 1978 to 1988 in Indonesia the number of birds that faced extinction increased from 14 to 126; and in Brazil from 29 to 121, of which 64 occurred in the largely destroyed Atlantic Coast rain forest.[289]

The discussion of minor forest products (section 10.3) showed that direct economic benefit is at stake. Contemporary human impact on rain forests and disappearance of traditional ways of life has led to a renaissance in ethnobotany, as a salvage operation to record traditional usages, and to renewed exploration for useful species. There are several products from rain forests which have recently begun to be exploited. Amongst these are a perennial teosinte, *Zea diploperennis*, discovered in late 1978 in relict forest in Mexico,[290] which has useful disease and pest resistance genes for the improvement of maize (*Zea mays*). There are many more opportunities still awaiting de-

velopment. For example, *Elaeis oleifera* is the South American congener of the African *E. guineensis*, the commercial oil palm. The Amazonian species offers a high quality oil, a lower height because of its creeping trunk, and better resistance to diseases.[291]

## Impoverishment of human societies

There are human societies throughout the tropics who live in, or are closely dependent on, the rain forest. These societies are destroyed if the forest disappears.[292] Other communities have their roots there and make use of many jungle products, and these are impoverished by forest destruction.

The nomadic Mbuti (pygmy) hunter-gatherers of the eastern Zaire basin Ituri forest in Africa use small forest-dwelling antelope (mainly five species of duiker, *Cephalophus*) as an important source of meat. The antelope populations diminish unless there are unhunted areas. Gregariously fruiting trees of Leguminosae/Caesalpinoideae are a major food, and are not found in secondary forest, so the antelope cannot survive where large areas of primary forest disappear.[293]

Recently, confrontations between forest dwellers and logging companies have taken place in Sarawak where rapid, high intensity logging had begun to destroy the dipterocarp rain forest home of nomadic Penan, and removed an important source of wild meat, rattans, cordage, and wood for many settled longhouse dwellers of other tribes. In the Amazon the few scattered Amerindians who have survived the centuries of attrition from outside are coming increasingly into conflict as dams, mines, farmers, road builders, missionaries, or gold prospectors move into their territory. Such peoples seldom have political muscle to prevent encroachment, or the skill and the contacts with mainstream society needed to seek redress.

The modern world creates manifold pressures, ultimately due to population increase (Fig. 10.1). As a result, traditional societies closely dependent on the tropical rain forest are experiencing many changes. This is epitomized by the village of Gunung Kemala in southern Sumatra (Fig. 10.11), as described from a visit in late 1987 by J. Mayer.[294]

On the hills above the village intermingled with relict rain forest are extensive mixed orchards, kebun, of fruits, spices, coffee and planted *Shorea javanica* trees[295] from which resin is tapped. The kebun is the backbone of the village's cash economy. During World War 2 it, and the wilder jungle beyond, provided a bare subsistence of fruits, roots, shoots, leaves, fungi, small game and fish, essential to supplement what rice was left after the occupying Japanese had taken their share. Trees for construction and firewood were felled under duress and full production was not restored until the mid 1960s when new trees matured. Population has grown rapidly recently and is about 4000 people today. In irrigated rice fields in the two river valleys two crops are now grown every year, new high yielding cash-hungry cultivars which depend on added chemical fertilizer. Shifting cultivation of the upland forest has also changed.

The transformation of the landscape around Gunung Kemala has occurred gradually, as people have cleared, burned off, and planted small fields rather than simply allowing natural secondary forest to reclaim the fallow fields. Hill rice is grown for three or even four years, then vegetables and other quickly maturing crops till ten years. Trees are planted for a huge variety of uses and these then take over. These means of converting the forest for human use maintain many of the ecological values of the original jungle and preserve natural catchment areas. Sugar palm, (*Arenga pinnata*), four kinds of useful bamboo and many fruit trees, including durian, are amongst the species planted.

There is still a lot of land available in the region, yet not everyone has access to padi fields, some people are completely dependent on hill rice. The possibility of opening new land for shifting agriculture, expanding a kebun, or in exceptional circumstances even burning off an old one, to grow staple crops provides a safety valve. As long as these alternatives for getting more land exist, they will probably prevent disastrous over-cultivation, and mitigate the potential for the growth of a substantial class of landless farmers. However, this security may come at the expense of the still-extensive old forests. The lands used as kebun and for hill rice are pushing ever farther into the old jungle, including primary forests. More and more frequently they are running up against lands claimed by other communities. The legally protected forest is being encroached upon. This slow expansion may eventually threaten the integrity of the primary forests, which have recently been declared a National Park.

And always the demand for cash increases: cash for better building materials, cash for motorcycles, cash for fertilizers and pesticides, cash for newly available com-

mercial medicines, cash for school fees, cash for cigarettes. In Gunung Kemala, cash comes from selling kebun produce, from raising chickens or goats, from relatives who have left, or from gathering rattan or resin.

The kebun and empty lands no longer supply enough of the firewood needed for cooking for the increasing population. Similar signs of population stress are familiar throughout the forest-dependent Third World. Many teenage girls walk as much as three hours from the village, several times weekly, to gather enough fuel for their families' needs. Once girls are big enough to carry a full load, the time-consuming search for firewood may cost them the opportunity to continue in school.

In the mid-1960s, the road inland over the mountains was unpaved. The village was virtually inaccessible except by sea. Now nearly all of the trade is by road, a rough twenty-hour trip. And much of that must still go through Jakarta before it is exported. Gunung Kemala's isolation is both a blessing and a curse. While the hills around it have protected the area from immigration, a dominant feature of much of the rest of the province, the village has also missed out on the convenience of improved infrastructure, paid for by the government. Roads crumble, bridges disintegrate through lack of maintenance, and old port installations slowly sink into the sea. But compared to much of the rest of the province, though pressure on land is gradually increasing, the area is remarkable stable.

After a week at Gunung Kemala the bus ride back over the mountains was a shock. Past the ridge, now largely protected as National Park, the forest was gone. Not just the jungle, but nearly all sizeable clumps of trees that grew a few years ago. While many of the areas for the next seventy kilometres or so had been cleared at one time or another it was the construction of the road that had dealt the final blow. Much of the ground was naked to the horizon, or dotted with new coffee and clove tree saplings. How long could the land stand up to the gullies that were taking over. Five years? Six? The buildings of the new settlements were thrown up in no recognizable tradition. It was amazing to realise the settlers from other provinces, who had moved in once the road was built, had been there only two or three years.

## 10.6. Rays of hope

There is a general vague but increasingly focused perception in the industrialized nations that tropical rain forests are under threat. This is largely due to publicity by the burgeoning conservation movements of the last third of the twentieth century for which the loss of the jungle has become a major issue. Tropical rain forests, which still seemed limitless in mid century, are becoming increasingly fragmented. The conservation movement has begun to force a broader vision, a return to a former wider view of tropical rain forests, by exerting democratic pressure on bilateral and multilateral aid agencies, so these are starting to change their attitude.

### The response detailed

The concern expressed on the loss of rain forests has elicited various responses.

*Aid agencies.* Several aid agencies in 1985 collaboratively produced the Tropical Forestry Action Plan (TFAP) to co-ordinate and rationalize their activities. This succeeded in doubling internatio-

nal aid to forestry from 1984 to $US $1 \times 10^9$ in 1987. It is, however, strongly focused on the timber values of forests, has been slow to incorporate an awareness of the importance forests have for indigenous peoples, and gives them little voice in deciding their own future. So far too, conservation has also received inadequate attention.[296]

Environmental impact assessments (EIA) are now usually required before funds are released for projects that will necessitate alteration of forests. Unfortunately, sometimes only lip service is paid to their findings. The objective of an EIA is to unravel the complex linkages in an ecosystem and see how a proposed development would affect them. It may then be necessary to modify the plans to reduce or eliminate bad consequences.

The floodplain of the Amazon shows how alteration of a forest may have totally unexpected but serious repercussions. The swamp forests which fringe the Amazon and its tributaries lie over alluvial soils, the most fertile in the basin and occupy $c.\ 10^5 \text{km}^2$. It is sometimes suggested that the land should be converted to agriculture, concentrated here not on the infertile *terra firme* (dry land)

oxisols and ultisols. Many Amazonian fish feed on the fruits of swamp forest trees (p. 71), and both rural and urban populations depend on fish as a major source of protein. Loss of the swamp forests would destroy an essential link in the ecosystem chain, fish populations would collapse, and much human suffering would ensue. There would also be serious repercussions on the hydrology of the river system because of the removal of floodwater storage capacity.

In the United States a series of amendments to the Foreign Assistance Act in the early 1980s broadened the mandate of USAID, the international aid agency, to include conservation of biological diversity and to reverse tropical deforestation. USAID projects now have a budget to fund these initiatives, albeit small and vulnerable to shifts in public opinion and political fashions.[297]

The observer has many reasons to be cynical concerning the actions of aid agencies. For example, a dam was proposed at Nam Choan on the Kwai Yai river in west Thailand. It would have cut through the big Thung Yai tropical moist forest wildlife sanctuary and eliminated much riparian habitat. The project did not receive World Bank funds because of the serious repercussions identified by an environmental impact assessment, only to be revived a few years later when Japan offered to pay. Fortunately over forty groups responded to the Deputy Prime Ministerial committee in Thailand which solicited public opinion and the renewed proposal was again defeated.[298]

Another activity funded by aid agencies has been to improve the productivity of agriculture on the inherently poor soils which predominate in the humid tropics. Scientists have analysed what makes shifting agriculture sustainable (section 8.1) and farming systems are being devised which exploit the nutrient-cycling capabilities of trees which underly it. The future may lie not in enhancing the efficiency but in building new agroforestry systems based on the fundamentals of shifting agriculture. Alley cropping, as one example, was mentioned on p. 144.

*Non-Governmental Organizations.* NGOs have set the agenda for rain forest conservation activities. The World Conservation Strategy[299] established the concept that conservation is the sustainable use of natural resources, plus the maintenance of their diversity, for mankind's continual future benefit.

NGOs have initiated major inventories of forests and their constituent species, for example IUCN produces Red Data Books on threatened and endangered species, and lists of National Parks and Equivalent Reserves. The revived interest in ethnobotany has led to the foundation of an Institute of Economic Botany at New York Botanic Garden (with, in 1988, a budget of $US 400 000).

In the late 1980s Friends of the Earth initiated an embargo within consumer nations[300] on the use of timber from rain forests that were not being exploited sustainably. It is more difficult for the NGOs of industrial nations to focus protests accurately about matters within producer nations. Potentially more powerful are the increasingly vocal local protests[301] (Figs. 10.23, 10.24). Alarm about what roads, dams, and pastures could to the Brazilian Amazon[302] has catalysed a national concern within Brazil on rain forest issues. In Brazil in February 1989 the Kayapo Indians came together for a massive public protest against dams proposed along the river Xingu which attracted worldwide publicity. The Malayan Nature Society has since 1970 fought off three separate threats to the country's main national park, Taman Negara (434 000 ha), and has attempted, so far unsuccessfully, to get a second large area (70 000 ha) decreed a national park at Endau Rompin, *inter alia* to protect the last remaining Malayan breeding herd of 20–25 Sumatran rhinoceros.[303]

Another innovation of the late 1980s was the introduction of 'debt swaps'. An NGO purchased part of a nation's international debt from the lender (at a discount) and in exchange the nation set an area aside for conservation. Bolivia, Costa Rica, and Ecuador were first and 'debt for nature' exchanges are also under discussion in Colombia and the Philippines,[304] and while this book was in press Madagascar followed (Fig. 10.25).

*National agencies.* Over 3000 national parks and equivalent reserves have been created in all parts of the world's tropical rain forests since the early 1970s, with a total area of 400 × 10^{6} ha.[305] This is a good start. For some, management plans have
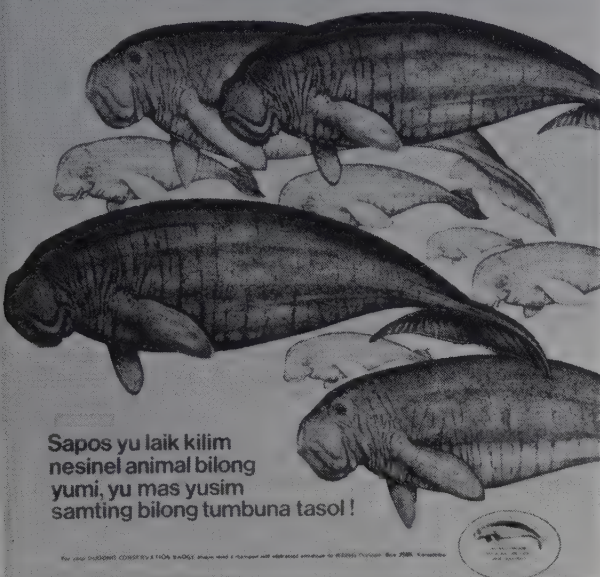
**Fig. 10.23.** Conservation poster. Papua New Guinea. (Gagné and Gressitt in Gressitt 1982.)

A literal translation of the Pidgin caption is 'Preserve the dugong for the future. If you want to injure our national animal [don't] behave as if there was a taboo'.

been written. Unfortunately though, in many cases the committment to conserve is solely on paper and there are no funds or staff to protect the areas from illegal encroachment or poaching. The Bali starling (*Leucopsar rothschildi*) diminished from 500 to 55 birds between 1978 and 1988 even though its rain forest home is the Bali Barat National Park.

In addition some rain forests have been registered as Biosphere Reserves with UNESCO, the body that invented the concept. A Biosphere Reserve consists of an inviolate pristine core surrounded by a 'buffer zone' of forest managed for sustainable production and may also include cultural landscapes of plantations, orchards, fields, and pastures. It exemplifies well the World Con-

servation Strategy concept of sustainable utilization with the maintenance of full diversity and species richness: man living in balance with nature.

UNESCO also has a World Heritage Convention. Thirteen areas of tropical rain forest (Table 10.13) and the outlying fragments of subtropical rain forest in New South Wales have been listed as World Heritage areas. In order to qualify for inclusion an area has to be of acknowledged universal value.

Furthermore, national planning of the zonation of rain forest lands which are to be opened up and settled is increasing. For example, in Amazonia, areas are allocated to different usages such as production forestry, extraction of minor forest products (so-called 'extractive reserves'), and for traditional inhabitants. Such plans are replacing the indiscriminate clearance which took place in the past.

*International Timber Trade Organization, ITTO.* This body was established by the United Nations in 1985 with 42 consumer and producer nations as members and with NGO observers.



**Fig. 10.24.** Conservation poster. Brazil. This, the most ape-like monkey of the neotropics and the largest endemic mammal of Brazil, is one of the many endangered species of the Atlantic Coast rain forest.

The Portuguese caption reads 'It's ours, the largest in the Americas, the Muriquí monkey'.

<center>Table 10.13</center>
<center>*World Heritage tropical rain forests*</center>

**Africa:**
Cameroon, Dja Faunal Reserve, 1987
Guinea and Ivory Coast, Mt. Nimba Reserve, 1981
Ivory Coast, Tai National Park, 1982
Zaire, Kahuzi-Biéga National Park, 1980
    Salonga National Park, 1984
    Virunga National Park, 1979

**America:**
Costa Rica, Talamanca Range and La Amistad
    Reserves, 1983
Honduras, Rio Platano Biosphere Reserve, 1982
Panama, Darien National Park, 1981
Peru, Manu National Park, 1987

**Eastern tropics:**
Australia, northeast wet tropics, 1988
India, Sundarbans National Park, 1987
Sri Lanka, Sinharaja Forest Reserve, 1988

The World Heritage Convention has been ratified by 102 countries and 65 natural sites have been inscribed on the World Heritage List. Thirteen of these are in tropical rain forest.

The 18 producer members together account for 95 per cent of all international trade in tropical hardwood. The aim of ITTO is to 'encourage sustainable utilization and conservation of tropical forests and their genetic resources'. ITTO is based in Yokohama, which is appropriate because 40 per cent of the annual £4.3 billion international hardwood trade involves Japan. In the words of the Japanese Foreign Minister[306] 'with regard to tropical rain forests we should strike a balance between environment as well as protection and development, to save the earth ... I would like to see both producer and consumer countries mutually join hands to actually find the solution to this problem'. As this book is being written ITTO is still establishing its priorities. It is a forum

**Fig. 10.25.** Advertisement of a 'Debt for Nature' swap in *The Economist* **312**, 7621, September 23, 1989.

where the different viewpoints can be expressed and positive moves made, a potential advance on the years of mutual recrimination between conservationists and those involved in the timber trade which preceded its establishment. A good start would be to increase the market price of tropical hardwoods, linked to sterner policing of logging operations, and thereby to give an incentive to reduce wastage.[307]

## 10.7.  Genetic resource conservation

The final factor that will help develop the future of wild genetic resources is their conservation. Breeders and genetic engineers can devise more and more ingenious ways of using available genes but they cannot create new ones. Although wild genes are a brand new resource and although their utility is growing dramatically, the lack of progress in conserving them ... casts a shadow over their future.[308]

There are two modes of genetic resource conservation with the ugly but descriptive appellations, *ex situ* and *in situ* conservation (Fig. 10.26).

## Conservation outside the forest

Storage off-site, or *ex situ*, can take several forms. Storage of seed in seed banks is only practicable for those species that have orthodox seed (p. 110). It has only been applied to a few major crops of the humid tropics, notably rice for which IRRI, the International Rice Research Institute, in the Philippines has 200 000 holdings (70 per cent traditional varieties, 10 per cent wild species); and to a few pioneer timber species, e.g. *Cordia alliodora* of northern tropical America and some subtropical pines (mostly *Pinus caribaea*, *P.oocarpa*). Genetic diversity can be represented in seed banks, but on-going adaptation to pests, diseases, biotic interactions, and climatic change then ceases. A few important plantation tree species have certain races ('provenances') conserved in plantations. In the case of some pines the original wild populations have now disappeared.

Arboreta and Botanic Gardens are less satisfactory for *ex situ* conservation because each species is represented by only a few individuals. The Botanic Gardens of the humid tropics were established as centres of trial and introduction but have become increasingly less relevant to the needs of agriculture and forestry. Botanic Gardens worldwide have recently awoken from a long slumber to realize that, like zoos, they may have a role to play in conservation, if only they can precisely define it. They have made a start to co-ordinate their activities and to compare stock inventories, and have established a Botanic Gardens Conservation Secretariat based at Kew and operated by IUCN.[309]

## Conservation within the forest

*Ex situ* conservation can never conserve more than a tiny fraction of the species richness of tropical rain forests. Conservation of species in place (or *in situ*) in the forest is much more important and is the best means of conservation of the numerous species that have recalcitrant seed (p. 111).

'Conserve adequate habitat' is the underlying principle and for every biogeographical region National Parks and comparable conservation areas can be supplemented by managed production forest.

Animal geneticists have given considerable thought to the question of how many individuals are necessary to maintain the full genetic integrity of a species in perpetuity.[310] Much has been learned from zoos. A simple but extremely crude rule-of-thumb is that a minimum population of 50 breeding adults maintains fitness in the short term, thus preserving a species 'frozen' at one instant of time. To prevent continual loss of genetic diversity ('genetic erosion') over the long term, and therefore to conserve the potential for con-

MOST
EFFECTIVE

```
                ┌─────────────────┐   ┌─────────────────────────┐
                │ Single use      │   │ Scientific reserves/    │
                │ wildland        ├───┤ strict nature reserves  │
                │ management      │   │                         │
                └─────────────────┘   └─────────────────────────┘
                                      ┌─────────────────────────┐
                                      │ National parks          │
                                      │ Natural monuments       │
                ┌─────────────────┐   │ Managed nature reserves │
  ┌──────────┐  │ Multiple use    │   │ Protected landscapes    │
  │ In situ  ├──┤ wildland        ├───┤ Resource reserves       │
  └──────────┘  │ management      │   │ Anthropological reserves│
                └─────────────────┘   │ Multiple use management │
                                      │ areas                   │
                                      └─────────────────────────┘
                ┌─────────────────┐   ┌─────────────────────────┐
                │ Areas           │   │ Converted land managed  │
                │ other than      ├───┤ for genetic diversity   │
                │ wildlands       │   │                         │
                └─────────────────┘   └─────────────────────────┘
                ┌─────────────────┐   ┌─────────────────────────┐
                │ Whole           │   │ Botanical gardens       │
                │ organism        ├───┤ Zoos                    │
                └─────────────────┘   └─────────────────────────┘
  ┌──────────┐                        ┌─────────────────────────┐
  │ Ex Situ  │                        │ Sperm, egg,             │
  └──────────┘  ┌─────────────────┐   │  and embryo banks       │
                │ Organism        │   │ Organ banks             │
                │ parts           ├───┤ Seed and pollen banks   │
                └─────────────────┘   │ Gene banks              │
                                      │ Tissue culture          │
                                      └─────────────────────────┘
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LEAST
EFFECTIVE

**Fig. 10.26.** Different ways genetic diversity can be conserved. (After Ledec and Goodland 1988, Fig. 2.1.)

tinuing evolution, requires a big population, and a minimum of 500 breeding adults has been suggested to be necessary. This 50/500 rule is only a very rough approximation and can differ widely between species. The numbers certainly need to be increased to allow for ecotypic differentiation and (as occurs in many plants) for overlapping generations and restricted gene flow (section 5.6).

Most difficult to conserve are animals (or indeed plants too) that live at very low population density (e.g. hornbills, tapir) and including top carnivores (e.g. jaguar, tiger), or that have large territories (e.g. gaur and elephant) (Table 10.14). If enough forest is conserved for these rarities then most plant species and the commoner animals will be adequately represented (Table 10.15). Conservation, means in practice, caring for rare species. There is no escape from the fact that even for common species numbers drop as forest is destroyed (Table 10.16), and in many cases this will mean there is a loss of genetic diversity.

Table 10.14   *Density of hornbills and primates in the Krau Game Reserve, Malaya, and areas estimated to support 500 individuals*

|  |  | Numbers | Area (km²) to support 500 individuals |
|---|---|---|---|
| Kuala Lompat, 200 ha lowland rain forest | | | |
| Hornbills: | Helmeted | 1 | 100 |
|  | Rhinoceros | 1 | 100 |
|  | Southern Pied | 2 | 50 |
|  | Black | 4 | 25 |
|  | Bushy-crested | 5 | 20 |
| Whole reserve, 537 km², lowland, lower and upper montane rain forest | | | |
| Apes: | Siamang | 1440 | 186 |
|  | Lar gibbon | 1568 | 171 |
| Monkeys: | Dusky langur | 7952 | 34 |
|  | Banded langur | 12298 | 22 |
|  | Long-tailed macaque | 2975 | 90 |
|  | Pig-tailed macaque | 2800 | 96 |

From Whitmore (1984*a*, Table 21.1)

## 10.8.  Management of tropical rain forests for conservation

There is a strong case for retaining parts of the rain forest inviolate, as natural reserves, kept intact for species to continue to interact between themselves and with the environment. These forests act as benchmark reserves against which change elsewhere can be monitored. Their usefulness is increased if they are surrounded by production forest, not cultivated land. The Virgin Jungle Reserves set up throughout Malaya by the Forest Department as compartments of Forest Reserves not to be logged are an example.[311] However, no developing nation can afford the luxury of 'locking up' more than a tiny fraction of its forest. Fortunately, there are good prospects for combining utilization with conservation.

**Management for multiple uses**

The possibility exists to manage rain forests for multiple purposes, to meet the needs of conservation as well as to produce useful products. But to retain the long-term benefits implied by conservation it is necessary to forgo some immediate cash profit. Multiple use involves compromises.

It was demonstrated in Chapter 7 that sustainable production of timber from a forest is certainly possible whilst maintaining most of the natural richness and diversity, so long as one operates within the limits of natural dynamics.

Low volume selective logging on a polycyclic system alters the forest least. The full plant species

Table 10.15
*Frequency of occurrence of species and genera of trees with horticultural or pharmacological potential in the rain forest of Ulu Kelantan, Malaya*

| | | Number per 40 ha | Area (km$^2$) to support 500 individuals |
|---|---|---|---|
| (a) With horticultural potential | | | |
| Anacardiaceae | *Mangifera* (machang) | 6.7 | 0.3 |
| Bombacaceae | *Coelostegia* (punggai) | 0.5 | 4 |
| | *Durio* (durian) | 3.7 | 0.5 |
| Euphorbiaceae | *Baccaurea griffithii* (tampoi) | 2.3 | 0.9 |
| | *Elateriospermum tapos* (perah) | 33.0 | 0.06 |
| Guttiferae | *Garcinia* (kandis, manggis) | 0.9 | 2 |
| Leguminosae | *Parkia* (petai, p. meranti) | 8.8 | 0.2 |
| Meliaceae | *Lansium domesticum* (langsat) | 0.2 | 10 |
| | *Sandoricum koetjape* (sentul) | 0.8 | 2 |
| Moraceae | *Artocarpus integer* (bangkong; chempedak) | 1.3 | 2.5 |
| | *A. lanceifolius* (keledang) | 18.0 | 0.1 |
| | *A. rigidus* (temponek) | 7.4 | 0.3 |
| | *A. scortechinii/elasticus* (terap) | 3.4 | 0.6 |
| Sapindaceae | *Nephelium lappaceum* (rambutan) | 5.9 | 0.3 |
| (b) With pharmacological potential | | | |
| Apocynaceae | *Alstonia* (pulai) | 0.8 | 2 |
| | *Dyera costulata* (jelutong) | 7.2 | 0.3 |
| Moraceae | *Antiaris toxicaria* (ipoh) | 0.5 | 4 |

From Whitmore (1984*a*, Table 21.2)
Figures quoted are for trees ⩾1.2 m girth. Survey 26 628 trees in a 676 ha sample of 10 100 km$^2$ of mainly lowland evergreen rain forest.

Table 10.16
*Estimated loss of primates in Malaya 1957–1975 due to reduction of forest area from 84% to 51%*

| | Population in 1958 | population in 1975 | Loss | Per cent loss |
|---|---|---|---|---|
| Apes: | | | | |
| Siamang | 111 000 | 48 000 | 63 000 | 57 |
| Gibbons | 144 000 | 71 000 | 73 000 | 50 |
| Monkeys: | | | | |
| Dusky langur | 305 000 | 155 000 | 150 000 | 49 |
| Banded langur | 962 000 | 554 000 | 408 000 | 42 |
| Silver langur | 6000 | 4000 | 2000 | 33 |
| Long-tailed macaque | 414 000 | 318 000 | 87 000 | 23 |
| Pig-tailed macaque | 80 000 | 45 000 | 35 000 | 44 |

From Mohd. Khan in Cranbrook (1988, Table 17.1)

complement is likely to be retained, but the proportion of light-demanding gap species, including pioneers, will increase. It is essential though to enforce laws to minimize the damage caused by logging and to prevent hunters, minor product gatherers, or farmers from entering along roads and causing damage, depletion, or destruction. Logging at this intensity is unlikely to eliminate many animal species (see p. 178). Knowledge of their ecology can be utilized to favour them. Inviolate patches should be deliberately retained. Hollow trees used as nesting sites, and plant species which are important for food, should also be retained, especially keystone species which provide food in times of famine (p. 64), for example strangling figs and woody climbers. More research is needed to identify these groups. It has been found in both East Kutai, Kalimantan, and Kuala Lompat, Malaya, that strangling figs grow most commonly on timber tree species,[312] so to maintain enough of them means forgoing some of the timber harvest.

Rural people commonly get much of their meat by hunting wild animals, so-called 'bushmeat' in West Africa. It has been shown in Sarawak that the rain forest provides *c.* 18 000 tonne of wild meat every year, which is equivalent to about 12 kg per person. The cost of replacing this from domestic livestock and fishponds would be prohibitive, about £25 million per year.[313]

Finally, if forest cover is retained so will the climatic influences of the forest, its evapotranspiration, albedo, and gas exchange. It was shown in Table 10.12 that bare earth has higher albedo, and reduced evapotranspiration. It also has lower water infiltration, particularly if compacted. It is important to minimize the area taken up by trackways, and also to construct these so as to minimize soil erosion.

The management of the rain forests of Queensland in the early 1980s most nearly approached these ideals until all logging was stopped at the time they were declared a World Heritage area (Table 10.13). The management regime that was practised there needs to be extended rapidly to other parts of the Eastern tropics where forest degradation is today very rapid, and to be copied in the neotropics as exploitation increases there.

In any scheme for managing a tract of forest for sustainable production it is absolutely essential that some patches are left inviolate in their virgin state. For, however careful human intervention to extract useful products may be, there is an inevitable alteration in the relative abundance and population structure of species, and usually also the simplification of forest structure.

## Forest plantations

Timber is produced cheaply in natural rain forests. The trees can be left to continue growth until market conditions are good. The numerous species have different properties and as the market changes different products can be sold. This cheapness and flexibility mean that there will always be a strong case for a tropical nation to retain part of its rain forest for timber production.[314]

There is also a case for plantations.[315] These are about thrice as productive, but much less flexible. They require a substantial initial cash investment and a prediction that there will be a suitable specific market at a particular future date. Moreover, timber plantations are in essence a form of longterm agriculture and, like agricultural crops, sooner or later fertilization is required (see pp. 141–3). Timber sold from plantations takes the pressure off natural forests as a source of foreign exchange. They should only be established on already degraded sites, never at the expense of good natural forest.

Most plantations in the humid tropics have been of pioneer species which produce low density, pale, soft timber. Only a handful of species are planted extensively and sooner or later most that have been tried have succumbed to a pest or disease and been dropped from the foresters' repertoire. There are very few quality hardwoods which have proved successful in plantations. The experience of Malaysia illustrates these points. There, plantations are being established to supplement timber production from the second cut of dipterocarp rain forests, which will be less than the first cut even assuming silvicultural rules have been closely followed.[316] Quality hardwoods (mahogany, *Swietenia* spp.), and lower value *Acacia mangium*, *Gmelina arborea*, and *Paraserianthes (Albizia) falcataria* have performed satisfac-

torily. Many other species have been commercial failures (e.g. *Anthocephalus chinensis, Araucaria cunninghamii, A. hunsteinii*: kadam, hoop pine, klinki pine). Far more thought and more trials are needed to find other quality hardwood species suitable for plantations. There will be a huge future demand for this sort of timber as the virgin forests become exhausted. Botanists and foresters need to get their heads together. One species ripe for investigation is *Pterocarpus indicus* (angsana, sena) of Malesia which has a very valuable, finely figured cabinet timber and fast growth, as witnessed in the garden city of Singapore where it is the most extensively planted shade tree.[317]

The current ratio of forest destruction to tree plantation establishment in the humid tropics is about 5 to 1 in Asia, 15 to 1 in America, and 30 to 1 in Africa. In some places this imbalance is begining to cause serious timber deficits particularly for fuelwood.

At Korup, Cameroon, plantations for fuelwood and constructional timber for the local people are being established as a buffer zone around the National Park, to reduce the pressure of traditional usages on the rain forest. A similar proposal has been made but not yet implemented for the important Gunung Leuser National Park in Sumatra.

The ground layer of tree plantations at Omu, Nigeria, were found to have one-third of the species of the rain forest, including many used by the rural population [chewing sticks (*Garcinia* spp.), cordage, and medicines][318] (see Fig. 10.27). It has been observed in Puerto Rico that once plantations have restored a forest canopy native species invade and eventually natural vegetation is restored. Species that take up larger amounts of mineral nutrients best facilitate this succession. Restoration of forest via plantations will be an important tool for the land manager of tomorrow.



**Fig. 10.27.** Plantation of Meliaceae (big tree, right) in Nigeria, which has developed a rich understorey of native species.

Natural forest can be restored via plantations and in Nigeria the understorey provides villagers with many useful plants. The plantation shown here, one of the Kennedy plots, was illegally felled in the late 1980s.

**Forest fragments**

Increasingly in the future, tropical rain forest will only survive as fragments. Some such already exist, for example Barro Colorado Island in Gatun Lake, Panama, Pasoh and Sungei Menyala in Malaya, Bukit Timah in Singapore, and Semengo in Sarawak. There is the problem that such fragments may break the 50/500 rule (p. 187) and contain too few individuals of a species for its long-term genetic integrity. Species that occur at low density are especially vulnerable either to genetic erosion or to chance extinction when numbers fall (p. 65). Moreover, small remnants may be too small to support top carnivores and this may have repercussions on other components of the ecosystem. For example, Barro Colorado Island, 16 km², no longer has puma or jaguar, although these big carnivores were present in the area before the Panama Canal was built and the island was created. Their prey species are only half to one-tenth as abundant as at Cocha Cashu, Peru, which is a very similar but huge forest, and these prey include seed-eaters, including the big rodents agouti and paca (Dasyproctidae). There is no evidence from Barro Colorado Island itself whether the huge increase in seed predators has affected forest composition but tiny islets (<2 ha) nearby in Gatun Lake, which are too small to support large vertebrate seed predators, have much higher abundance than the nearby mainland of big-seeded palms (*Astrocaryum, Oenocarpus, Scheelea*) and trees (*Dipteryx, Protium*).[319]

Pasoh forest has lost the animals which once dispersed the seeds of *Chrysophyllum lanceolatum*, and, as was described in section 5.5, today piles of rotting fruit accumulate below the parent trees.

Besides reduction in area, forest fragmentation also increases the proportion of edge relative to interior and if the fragments are surrounded by open land this will result in a change of micro-climate.

Forest conservation will increasingly require active management to circumvent these deleterious effects. Much more research is needed on interactions before we really understand how ecosystems are constructed and work. To identify keystone species (pp. 64, 73) is crucial. We can take heart from Bukit Timah on Singapore. This is only 71 ha and has been a relict patch of mainly primary forest for about 100 years. Yet it still looks like a dipterocarp rain forest, and has over 800 plant species, even though about half of the mammals and birds have been lost.[320] Until 1985, when a motorway was built, Bukit Timah had a big contiguous secondary forest hinterland, which perhaps contributed to its resilience. It seems probable that ecosystem functioning will have changed at Bukit Timah, for example that birds now disperse fruits previously dispersed by mammals. A fascinating and unexplored field of research is to investigate whether such changes do take place in rain forest fragments and if so whether the ecosystem can continue to function either as it is or differently. To what extent are plant-animal interactions closely knit and to what extent opportunistic but with the same or similar end result (cf. p. 96)?

Land use pattern can mitigate the consequences of forest fragmentation. Inviolate forest set in a mosaic with production forest and tree plantations, and the linking of forest patches by corridors through agricultural land are all likely to help maintain wild species. Again, research is needed before sensible plans can be made.[321]

For a consideration of whether this optimistic scenario will indeed be realized the reader is referred to the epilogue.

## 10.9.  Tropical rain forests yesterday, today, and tomorrow—Chapter summary

1. Human societies in many parts of the humid tropics, be they hunter-gatherers, shifting cultivators, or settled farmers, have developed in close dependence on the rain forests.

2. The colonial era had a profound impact on tropical societies, some disappeared but left tell-tale traces in forest structure or species composition which are now being discovered. The spice

trade shaped the history of the world. Useful plants were moved between continents and introduced to their new region via Botanic Gardens. Today, staple foods and many fruits are pan-tropical as a result. The Industrial Revolution increased demand for many forest products such as rubber and resins. Only recently has trade in these minor forest products been overtaken by that in tropical hardwood timber.

3. Tropical woody vegetation is being altered at a rapid rate (Table 10.5), in one of two different ways. Some areas are converted to other use, others are logged but left to regenerate, though these latter are often later destroyed by people moving in along the roads built by loggers. There are major differences between regions in the rate at which tropical moist forests are disappearing (Table 10.6).

4. Forests are destroyed to make way for agriculture. This takes several forms and there are major differences between regions.

5. One class of agricultural activities is planned by government. Pastures for cattle are most important in the neotropics. Tree plantations producing export crops (mainly oil palm and rubber) are most extensive in the Eastern tropics. Plantations for wood production occur everywhere. Agricultural smallholdings created by government are also important especially in the East, for example transmigration in Indonesia.

6. The other class of agricultural activities is unplanned. In many countries peasant farmers are moving into rain forest, usually to practise shifting agriculture and often illegally. In some places there is an advancing frontier of destruction progressing through the forest (Fig. 8.3).

7. Forests are also destroyed for dams and mines.

8. Forests are utilized without being destroyed in various ways. Fuelwood comes mainly from seasonal forests (because most people live in seasonal climates). Industrial wood (timber, fibres) comes mainly from rain forests. Production of tropical hardwoods has increased greatly since 1950 and may continue to rise (Fig. 10.21). Asia is the main contemporary source and dipterocarp rain forests are peculiarly suitable both for exploitation and renewal. Wood chips are only produced in three dryland rain forests, more comes from mangroves.

9. Rain forest bird and small mammal populations have shown surprising resilience to logging in the three forests studied so far, but repeated logging might be more deleterious.

10. Interference with rain forests might affect climate by decreasing rainfall or heat absorption or by increasing 'greenhouse' gases ($CO_2$, methane, oxides of nitrogen). A change to bare land (which is unlikely over big areas) has greatest effect, to pasture less, and to a different woody vegetation least effect. The overall change to global climate is imponderable but probably less than sometimes claimed.

11. Human interference reduces the biodiversity of rain forests by causing simplifications in structure and by loss of species.

12. Human life is impoverished by forest loss, especially for the rural people who live in or near the forest.

13. The loss of rain forests has become a major issue for burgeoning conservation movements. In the industrial world these have begun to force aid agencies to adopt a broader vision and to view forests as a source of many goods and services not just as timber quarries. National conservation groups in rain forest countries have also begun to exert pressure.

14. The genetic resources of rain forests can be conserved *ex situ* in seed banks, or living collections, but for many species, especially those with recalcitrant seeds, conservation in the forest *in situ* is the only realistic possibility. An adequate population must be conserved, and a *very* rough rule is 50 breeding individuals short-term, 500 long-term.

15. The management of tropical rain forests is an important tool for their conservation. Rain forests can be managed for multiple uses, to produce timber and minor forest products, and to continue as animal habitat and with the full complement of plant species. Inviolate bench-mark reserves are essential, as part of a mosaic of different kinds of land use. Forest plantations take the pressure off natural forest as a timber source.

16. Forest fragments, if isolated, degenerate by loss of animal pollinators, dispersers, and predators. The species balance is upset. Active management will be an increasingly important precondition for conservation as rain forests are increasingly fragmented. Research to understand how they work is essential.

# Epilogue

## Epilogue

We live in an interesting Age. What will our descendents think of us as they look back? All is not yet lost of the world's tropical rain forests but it is difficult to be optimistic about their future.

Some parts of the rain forest have been irretrievably lost. I write this in Singapore, and have recently made several visits to the adjacent southern tip of Malaya, south Johor. Rain forest has been virtually eliminated from the landscape there, starting with gambir cultivation last century and continuing with agricultural settlement and logging for timber this century. Even if species-rich forest were restored on cleared land the local endemics are now extinct. The driving force for forest destruction is frequently immediate, tangible profit—money (sometimes in a numbered Swiss bank account). Will this short-term profit be foregone for the less tangible long-term benefits? Man's cupidity, his desire to get rich quickly, is not compatible with the longer horizon of sustainable use of the forest. Are the voices questioning the get-rich-quick philosophy being heeded fast enough? There are encouraging signs, but is conservation happening too little and too late?

The underlying message of this book is that tropical rain forests are a renewable resource which can be utilized and still retain their diversity and richness for mankind's continuing benefit; but only if we care to learn enough about how they work, and also if, as has been repeatedly stated, utilization takes place within the limits of the forest's inherent dynamic processes.

The lives of our children and grandchildren will be poorer if most or all of the tropical rain forest disappears; much more so than from the loss of any other biome. This book will have achieved its purpose if it illuminates the discussion on this great issue and enables the rising generation in all parts of the world to do better than their recent forebears in making intelligent decisions.

# Text notes

1. There is also a torrent of new scientific publications. For fuller reading than in this book the whole subject of tropical rain forests is covered in two comprehensive accounts. Richards (1952) is the classic text. It is still in print and synthesizes the work of European scientists in tropical rain forests up to about 1940. Whitmore (1984*a*) is the only modern comprehensive book on tropical rain forest ecology. In it most of the subjects covered in the present book are discussed in great detail and with examples drawn from the Eastern rain forests. Some topics have developed fast in the 1980s, but apart from those this is the best general reference for further reading. On a more popular level Ayensu (1980) is one of the best of the plethora of quasi-scientific books aimed at the concerned layman. Mitchell (1986) and Richards (1970) are beautifully illustrated general introductions. Other sources of more detailed information are referred to later in these text notes.
2. See Putz and Holbrook in Denslow and Padoch (1988) for an analysis of the influence tropical rain forests have had on European culture.
3. Stearn (1977) as paraphrased by Mabberley (1988).
4. *Antiaris toxicaria*, in modern Malay called ipoh.
5. Burkill (1935).
6. Quoted in Merrill (1945).
7. *Caesalpinia pulcherrima*.
8. A. R. Wallace quoted by Richards (1952).
9. *Verbena officinalis*.
10. *Aesculus hippocastanum*.
11. *Polygala vulgaris*.
12. *Vinca*.
13. *Viola*.
14. R. Spruce writing on the Amazon and quoted by Richards (1952). He uses as examples plants of northwest Europe likely to be known to his readers.
15. In this book the term canopy is used for the whole forest, not just its upper surface.
16. Corner (1964).
17. Whitmore (1989*c*).
18. Richards (1952).
19. A remarkable twentieth century recapturing of nineteenth century science, recorded amongst other species by: *Whitmorea grandiflora*, *Allowoodsonia*, *Bridelia*, *Calamus*, *Endiandra*, *Freycinetia*, *Heliciopsis*, *Horsfieldia*, *Macaranga*, *Mangifera*, *Pandanus*, *Piper*, *Rhododendron*, *Terminalia*, and *Vaccinium whitmorei*.
20. Sommer (1976).
21. Walter and Lieth (1967).
22. Hueck and Seibert (1981); UNESCO (1981).
23. These figures are for potential extent, viz. the area covered before Man came on to the scene.
24. Whitmore (1984*b*).
25. Whitten *et al.* (1984, 1987) are two important regional accounts published, in both English and Indonesian, on the ecology of the Indonesian islands of Sumatra and Sulawesi, respectively. They are at the same time student textbooks and source books for researchers.
26. Webb (1968).
27. Whitmore (1982*b*).
28. White (1983).
29. White (1983).
30. Baur (1968), White (1983).
31. Whitmore (1982*b*).
32. For references see Whitmore (1984*a*).
33. Van Steenis (1972) is an elegant illustrated account.
34. See White (1983).
35. Brunig in Ashton (1971).
36. Davis and Richards (1933–1934).
37. Ramin (*Gonystylus bancanus*), with timber pre-eminent for mouldings, grows here.
38. Watt (1947): Whitmore (1978, 1982*a*, 1988).
39. Kramer (1933).
40. Swaine and Whitmore (1988).
41. Some authors have talked about 'mature phase species' but that is to confuse the forest growth cycle, which concerns forest structure only, with the species of which a growth cycle is composed.
42. Bormann and Likens (1979).
43. Johns (1986).
44. Garwood *et al.* (1979).
45. Whitmore (1988, 1989*a*).
46. *Diospyros virginiana* (America), *D. kaki* (Orient).
47. Gentry (1988*a*) gives a comprehensive analysis.
48. Ashton (1982).

49. See Richards in Meggers *et al.* (1973).
50. Whitmore (1977*b*).
51. Hall and Swaine (1976).
52. Grubb (1987), excluding 'critical' species of *Sorbus* in Europe and including 5 and 23 species of conifers, respectively.
53. Ng and Low (1982) document this for Malaya.
54. Gentry and Dodson (1987).
55. P. J. Grubb (personal communication).
56. Whittaker (1972).
57. Whitmore (1984*a*) discusses this problem more fully, using Far Eastern examples.
58. Richards (1952).
59. Whitmore (1974).
60. We do not know why rheophytes are commoner in some places, or why only a few families have evolved them (van Steenis 1981). One family Podostemaceae consists entirely of rheophytes. It has 50 genera and 275 species and is largely tropical. Members of Podostemaceae are remarkable moss-like or thalloid plants with minimal or no vascular tissues, which cling by adhesive roots to fast-flowing rocky cataracts. They die back at low water. Most are tiny, but a few develop flowering seaweed-like flowering scapes to 0.6 m tall. It is always interesting to search for podostems while floundering up a rocky tropical stream. By keeping his eyes open Dr. J. Dransfield in 1968 made the first discovery of the family in Malaya, at a locality that had been much visited by botanists for 80 years.
61. Whitmore (1973*b*).
62. Newbery *et al.* (1986, 1988).
63. Evans (1972).
64. Sometimes known as screwpines.
65. Jacobs (1988).
66. Gentry (1988).
67. Holttum (1955).
68. Hallé and Ng (1981).
69. Hallé *et al.* (1978).
70. Henwood (1973) in Whitmore (1984*a*).
71. Corner (1988).
72. formerly *Tristania*.
73. Symington (1943); Whitmore (1972, 1973*a*); Ng (1978, 1989).
74. Klinge (1973).
75. For an excellent review see Ng (1984).
76. Ng (1984) and Longman and Jenik (1987) give clear accounts.
77. Holttum (1940) in Ng (1984).
78. Medway (1972a).

79. Reich and Borchert (1984).
80. R. T. Corlett, personal communication.
81. Janzen (1976).
82. R. T. Corlett, personal communication.
83. Holttum (1954).
84. Ashton *et al.* (1988) found that 5–8 nights with uniquely low minimum temperature of 18.9°C, not the usual 21–23°C, had occurred 8–9 weeks before a series of mass flowerings in Malaya and deduced that this chilling caused young, undifferentiated buds to become inflorescences not leaf flushes. However, this trigger did not precede the 1987 mass flowerings in Singapore and Danum, Sabah (R. T. Corlett and N. D. Brown, personal communication).
85. Bourlière (1983, 1985), Leigh *et al.* (1983), Montgomery (1978), and Terborgh (1983) give general accounts.
86. Erwin (1982). See also May (1988).
87. Stork (1988) later argued that the figure lies between 10 and 80 million species. J. B. S. Haldane, on being asked what he inferred of the Creator from a study of the natural world, replied that God must have an inordinate fondness for beetles. Erwin's study confirms this.
88. Terborgh and van Schaik (1987) describe these differences more fully and relate them to differences in the phenology of leaf and fruit production in the three regions.
89. Bourlière (1985).
90. Terborgh (1983, 1986). Charles-Dominique *et al.* (1981) made an equally elegant study for nine nocturnal frugivorous mammals in a secondary forest in French Guiana.
91. Terborgh (1983).
92. Leighton and Leighton in Sutton *et al.* (1983).
93. See Faegri and van der Pijl (1979) and Howe and Westley (1988).
94. Analysis has shown that species differ substantially in the composition of their nectar. Sometimes it contains amino acids as well as sugars. Intricate relationships have been discovered between nectar composition, amount and time of production, and the particular animal pollinators to which it is offered as an attractant and reward.
95. Appanah and Chan (1981).
96. Gould (1978).
97. Start and Marshall (1976).
98. See van der Pijl (1982) and Howe and Westley (1988).
99. Snow (1981).

100.  Terborgh (1983).
101.  Goulding (1980).
102.  Snow (1966).
103.  To a plant-eating animal 'the plant world is not coloured green; it is coloured morphine, caffeine, tannin, phenol, terpene, canavanine, latex, phytohaemagglutinin, oxalic acid, saponin, and L-dopa ... a many textured landscape of scents and tastes, the distinction of which may be a life and death matter' (Janzen in Montgomery 1978). Howe and Westley (1988) give a broad review of herbivory, the various defences plants have set up, and how animals overcome them.
104.  For example, the pretty Apocynaceous garden herb *Catharanthus roseus*, the rosy periwinkle, contains the alkaloids vincristine and vinblastine, valuable in the treatment of two previously intractable cancers. This species is a native of semi-arid Madagascar but is now pantropical. It commonly escapes and becomes naturalized on sandy shores.
105.  Gilbert (1980). He used the term 'food web' not 'plant web' which is confusing to zoologists who use the term in a different sense in discussions of trophic levels.
106.  The indications from those comprehensive studies that have been made are that fewer than 10 per cent of all plant-eating insects feed on more than three different plant families (Bernays and Graham 1988 in Strong 1988).
107.  Gilbert (1980).
108.  Appanah (1985). This pattern must have developed since human activity reduced Pasoh to an isolated patch. *Melastoma* dominated scrub is neither extensive nor common in the primary forest landscape of Malaya.
109.  Prance (1986).
110.  See Ehrlich and Raven (1964), Futuyma and Slatkin (1983), Thompson (1986), Strong (1988), and Howe and Westley (1988) for overviews.
111.  The hypothesis takes its name from the Red Queen who made this statement in *Alice through the looking glass*, a famous children's story by Lewis Carroll.
112.  Coley (1983).
113.  Huxley (1978).
114.  Kleinfeldt (1986).
115.  Fiala *et al.* (1989) *Oecologia* **79**, 463–70.
116.  Maschwitz *et al.* (1984).
117.  Benson *et al.* (1976).
118.  Ng in Sutton *et al.* (1983).
119.  Fedorov (1966); Ashton (1969). See also Whitmore (1984a) for a detailed account of the subsequent observations sketched here which have been made to flesh out the speculations.
120.  Kaur *et al.* (1978).
121.  Bawa (1974); Ashton (1969); Bawa *et al.* (1985a, b).
122.  Gan *et al.* (1977, 1981).
123.  See Hallam (1973) for a lively survey.
124.  Smith and Briden (1977).
125.  In the 1970s, *Pakairamea* was discovered growing on the Guiana Shield in Guyana and Venezuela. It is believed by some to be a third subfamily of Dipterocarpaceae, though others place it in Tiliaceae.
126.  Thorne in Meggers *et al.* (1973); Thorne (1977).
127.  Hallam and Audley Charles (1988); Whitmore (1981, 1987).
128.  Flenley (1979) gives a comprehensive synthesis.
129.  Haffer in Whitmore and Prance (1987) reviews geoscientific evidence for past different climates.
130.  Fig. 6.10 shows only the upper part of this record.
131.  Thorne (1977), van der Hammen and van der Cleef (1983).
132.  Richards in Meggers *et al.* (1973).
133.  Takhtajan in Whitmore (1987).
134.  See Brown in Whitmore and Prance (1987) for a critical review of neotropical Pleistocene refugia.
135.  Haffer (1967, 1974) for birds, Vanzolini (1970) for lizards: cited by Brown in Whitmore and Prance (1987).
136.  Hamilton (1976, 1982); Mayr and O'Hara (1986); Maley (1987).
137.  Hu (1980).
138.  Medway (1972b).
139.  van Steenis (1972).
140.  Luping *et al.* (1978).
141.  For overviews on tropical rain forest dynamics see Whitmore (1978, 1982a, 1988, 1989a).
142.  Platt and Strong (1989).
143.  Few observations have been made; some studies do show drier soil in gaps but others show drier soil below the closed canopy and this must be because the plants are withdrawing water from the soil and transpiring it.
144.  Swaine and Whitmore (1988).
145.  Budowski (1965).
146.  Egler (1954).
147.  Symington (1933).
148.  Keay (1960).

149. Whitmore (1983).
150. Roberts (1973).
151. Roberts (1973).
152. Burgess in Whitmore (1984a).
153. Howe and Smallwood (1982); Clark and Clark (1984).
154. Chan (1980).
155. Burgess (1969).
156. Discussed in detail for rain forests by Whitmore (1975) and then for vegetation in general by Grubb (1977).
157. Riera (1985); Raich (1987).
158. Brandani *et al*. (1988).
159. Connell (1978).
160. Chazdon and Pearcy (1986a, b).
161. Becker in Sutton *et al*. (1983).
162. Johns R. J. (1986).
163. Salo *et al*. (1986).
164. The ocean-surface warming altered currents throughout the Pacific and that is what altered the rainfall; see Gill and Rasmusson (1983) for a full description. One result was the changed position or oscillation of the current which strikes the coast of Peru about Christmas time. This change reduced the harvest of anchovies, mainstay of the local fisheries. The term El Niño is Spanish for 'The Child' and is an allusion to the Christ child, who was born at Christmas time.
165. Beaman *et al*. (1985).
166. Leighton and Wirawan (1986). In logged forest, by contrast, more of the small trees were killed.
167. Hubbell and Foster (1990).
168. Sanford *et al*. (1985).
169. At the seasonal-climatic margin of rain forest fire may determine its limit. In Queensland rain forest is today invading the adjacent dry sclerophyll forest dominated by *Eucalyptus grandis* (Fig. 2.6) because there are no longer aborigines to set fires. And in Ghana the northern edge of the rain forest burns in unusually dry years, such as 1982–1983.
170. Today gutta-percha is used only for temporary dental stoppings for which it is well suited by its unusual property of swelling as its sets from the liquid to solid state.
171. The term ecology is usually dated to the German E. H. Haeckel, 1866.
172. Technically termed the 'dysgenic effect'.
173. Economists commonly also fall into the pit of failing to put a value on everything else the forest provides in addition to timber.
174. For example, Baharuddin (1988) demonstrated this in central Malaya. In Queensland such cross-drains are evocatively named 'whoaboys'.
175. Schmidt (1987) reviews silviculture throughout the humid tropics.
176. See Whitmore (1984a) and Salleh in Cranbrook (1988) for fuller descriptions of silviculture in Malaya. In its full form the Malayan Uniform System included repeated interventions during the first decade after felling to assist growth of the next timber crop.
177. In Sarawak a highly modified form called Liberation Thinning has been introduced in which after logging very selective thinning is applied just around potential crop trees.
178. Fearnside (1989) reviews the handful of examples.
179. de Graaf (1986); Gradwohl and Greenberg (1988).
180. Nicholson (1965) and McWirter (1980) in Whitmore (1984a).
181. Guevara *et al*. (1986).
182. Kochummen and Ng (1977).
183. Hall and Swaine (1976).
184. Swaine and Hall (1988).
185. Whitmore (1974).
186. Jones (1955–1956).
187. Manokaran (1988).
188. Whitmore (1989b).
189. Zinke *et al*. (1978).
190. And was in fact also practised in prehistoric Europe.
191. D. U. U. Okali (personal communication).
192. Chin (1985).
193. Boerboom and Wiersum (1983); Denslow and Padoch (1988).
194. Kunstadter in Denslow and Padoch (1988).
194a. Uhl and Jordan (1984).
195. Ramakrishnan in Proctor (1989).
196. Jordan (1985) is the only comprehensive text and Proctor (1989) reports an important symposium.
197. Bruijnzeel (1989).
198. Baillie and Ashton (1983); Baillie in Proctor (1989).
199. Turvey (1974); Bruijnzeel in Proctor (1989).
200. Vitousek and Sanford (1986).
201. Proctor (1984).
202. viz. $k$ the decay factor ranges from 3 to 1, a turn-over thrice to once a year (Table 8.3).
203. Collins in Cranbrook (1988).
204. Gillman *et al*. (1985).
205. Poels (1987).

206. Refinement is the elimination, usually by poison-girdling of unwanted relict trees.
207. Gradwohl and Greenberg (1988) give an account.
208. Ecosystem nutrient capital in a plantation changes with age but is also likely to vary across the plantation due to intrinsic site differences. This makes it difficult to interpret data on nutrients against age put together from different sites.
209. Fearnside (1988) gives a good review of the Jari plantation forest project which covers *c.* 100 000 ha.
210. P. Lavelle (personal communication).
211. Kellman (1970).
212. The Yurimaguas experiment has been critically appraised by Fearnside and others (Fearnside 1987). The Nigerian work is described by Juo and Kang in Proctor (1989).
213. Jordan (1987); Gradwohl and Greenberg (1988).
214. Juo and Kang in Proctor (1989).
215. Fuller discussion and references to the research literature mentioned here can be found in Whitmore (1984*a*, 1991).
216. Medina and Cuevas in Proctor (1989).
217. i.e. the cation exchange capacity drops to nearly zero.
218. See Whitmore (1984*a*, 1989*d*) for fuller details.
219. The fullest study yet made of upper montane forest is in Jamaica. It was found that soil nutrients are adequate for growth and during the rather short study period water was not limiting. See Tanner (1985).
220. See also Whitmore (1984*a*) and Diamond (1988).
221. Whittaker (1977).
222. Strong (1972) in Whitmore (1984*a*), referring to photographs taken by the first men on the moon.
223. For the wider issues pertaining to mankind's disequilibrium with the resources of the planet see the Bruntland Report (World Commission on Environment and Development 1987) which includes discussion of forests and sets them in the wider perspective.
224. The forests of northeast Siberia and the great valleys that penetrate the Tibetan plateau westwards from China are the others.
225. Europe, Japan, and North America each take about one-third of the tropical timber that enters international trade: Thomson in McDermott (1988). Nectoux and Kuroda (1989), received after this book went to press, give a full analysis of the dominant role of Japan in the international tropical timber trade.

226. Britain's Overseas Development Administration alone gave £7.5 million forestry aid in 1987, doubled since 1983: Howard in McDermott (1988).
227. Made clear by the contributors to a Symposium at Yale (Mergen and Vincent 1987).
228. Renamed World Wide Fund for Nature in some countries.
229. Jacobs (1988) is a well-argued *cri de coeur* on this point.
230. Denslow and Padoch (1988) give a beautifully illustrated modern account.
231. Who have not discovered how to make fire and have to keep naturally occurring fires alight.
232. All lie in seasonal climates. One may speculate that permanent agriculture was easier and diseases less serious than in the perhumid tropics which have no dry season.
233. Balée (1987).
234. See also Peluso (1983) on the breakdown of social control on rattan exploitation in East Kalimantan after commercial logging began.
235. Purseglove (1968).
236. Merrill (1945).
237. Whitmore (1977*a*).
238. And in the Dutch East Indies a network of Nature Reserves was created half a century before these became widely used as a conservation measure.
239. Carneiro in Denslow and Padoch (1988) estimates that the population was 6 million when first discovered by Europeans around 1500 and has declined to quarter of a million today.
240. Anderson *et al.* in Lugo *et al.* (1987); Balée (1988).
241. See Rambo in Cranbrook (1988) on Malaya.
242. These are less biodegradable, hence the permanent mounds of rubbish which today disfigure so many tropical settlements.
243. The estimated plant-based prescription drug market of OECD countries (which make up most of the developed western world) was $US 43 billion in 1985, 41 per cent of the total market (Collins in McDermott 1988).
244. Even more remarkable, several species of *Brosimum* in Amazonia have a white, freely flowing latex which can be drunk and is used as a substitute for milk.
245. Cocoa entered cultivation in Central America where it was believed to be of divine origin (the scientific name *Theobroma* is Greek for food of the Gods). Amongst the Aztecs only the wealthy drank cocoa.

246. Recently wild-type coconuts have been found in both Australia and the Philippines, finally settling the old conundrum of where this species, 'nature's greatest gift to man', originated (Guezo and Harries 1984; Buckley and Harries 1984 in Uhl and Dransfield 1987).
247. Corner (1966).
248. Peluso (1983).
249. Rotan irit, *Calamus trachycoleus*, is especially suitable, and has been grown by villagers in the remote interior of central Kalimantan for over a century; over 7000 ha are now planted in Sabah (Dransfield 1988).
250. Fearnside (1989) analyses this problem.
251. These figures are controversial and might be overestimates because a fire anywhere within it causes a whole satellite pixel to be recorded burned. Fearnside (1990) considers $3.5 \times 10^6$ ha lost from all causes more likely.
252. Browder (1988); Uhl *et al.* (1988).
253. Hecht *et al.* (1988).
254. Cattle raised on tropical American pastures have lean, tough meat. Some of it is sold to North America. It is very suitable for hamburgers. For this reason rain forest destruction has been evocatively ascribed to 'the hamburger connection'. It is, however, totally misleading to regard the 'fast food' market as a major engine of Amazon deforestation. In 1982 hamburger-bound beef imports to the USA from nine Latin American countries were only 7900 t (*c.* 26 000–32 000 carcasses representing at the most 100 000 ha of pasture). This was 1.2 per cent of total beef imported to the USA where total beef consumption was 24 million tons (Browder 1988).
255. Fearnside (1988).
256. Federal Land Development Authority.
257. See Davis in Denslow and Padoch (1988) for an account of transmigration and its effect on the forests of Indonesia.
258. See Vayda in Denslow and Padoch (1988).
259. During the 1980s Stewardship Certificates were introduced, issued to shifting cultivators illegally occupying forest land, in an attempt to contain the problem by reducing their mobility. By 1988 175 000 certificates had been involved covering 600 000 families.
260. Though not yet paved as this book goes to press.
261. Lanly (1982).
262. Gray (1987).
263. Hong (1987).
264. Stone in Denslow and Padoch (1988) gives a full account.
265. Consumption will be $1 \times 10^6$ tonne charcoal $year^{-1}$ to fuel 7 pig iron, 21 iron alloy, and 2 cement factories already approved; 13 more pig iron plants await approval and a further 10 are being planned (Gradwohl and Greenberg 1988; Fearnside 1989*b*).
266. Roughly speaking, 50 per cent of the human race gets 90 per cent of its energy from fuelwood.
267. Full discussion is beyond the scope of this book but it can be noted that in much of the seasonal tropics fuelwood is becoming hard to get. In Karnataka, India, its cost increased eleven-fold from 1970 to 1988, compared to an overall rise in the cost of living of under four-fold.
268. With teak a major exception.
269. Gills in Denslow and Padoch (1988) describes the exploitation of the west Malesian dipterocarp rain forests.
270. The Philippines resource will run out *c.* 1995 and Peninsular Malaysia before then.
270a. Uhl and Vieira (1989).
271. The mahogany which was so important and fashionable as a cabinet timber in nineteenth century Europe came from the Caribbean (*Swietenia mahogoni*) and Central America (*S. macrophylla*).
272. 1 ha of forest has 200–300 tonne of wood, 4 tonne make 1 tonne of charcoal, and this fuels a smelter for 5 minutes.
273. Johns A.D. (1986).
274. Reviewed by Bruijnzeel (1986). Abdul Rahim (1988) showed 1.6- and 4.7-fold increases in water yield under 2- to 4-year-old cocoa and oil palm compared to natural rain forest, and predicted a decline as the crops matured.
275. The Rio Nima in Colombia is an example of a formerly forested water catchment where reestablishment of vegetation and the control of erosion has improved water quality, in this case for the downstream city of Palmira (Gradwohl and Greenberg 1988).
276. See Bruijnzeel (1986).
277. Salati and Vose (1984).
278. Dickinson and Henderson Sellers (1988).
279. See Bolin *et al.* (1986) for a general account.
280. Also man-made chlorofluorocarbons (CFCs).
281. Atmospheric $CO_2$ has increased 20 per cent, from 280 parts per million before the Industrial Revolution to 340 ppm in 1987. Most comes from burning fossil fuel, but there is also a substantial component due to land use change, which is nowadays mainly in the tropics. Carbon dioxide enters the atmosphere when forests are

destroyed, partly from burning the wood, partly from a reduction in the amount of soil organic matter. Estimates of the amount, which are difficult to make, vary for 1980 from 0.4 to 2.5 × $10^9$ tonne of carbon, which is from 8 to 50 per cent of the contribution from burning fossil fuel, a mean value of 29 per cent (Postel and Heise 1988).

282. Pearce (1989); 33 l = 200 g at room temperature.
283. For example, low-level layer clouds are highly reflective so have a big effect on heat balance.
284. The only exceptions are those forests where dead matter accumulates as peat instead of decomposing, or where degradation is by fire and incomplete combustion produces charcoal which is an inert material.
285. May (1988).
286. Cocoa, *Theobroma cacao*, an understorey tree of lowland rain forest, which is endemic to northeast Peru and adjacent Ecuador in the upper Amazon, is currently losing diversity as oil prospecting, logging, and settlement are eating away its habitat.
287. Simon (1986).
288. Simberloff (1986) cited by Postel and Heise (1988). The calculation is based on the relationship between size of an area and the number of species it contains as described by the theory of island biogeography of MacArthur and Wilson (1967).
289. Anon. (1988).
290. Iltis *et al.* (1979).
291. Kahn (1988).
292. Many examples are given in Denslow and Padoch (1988), Anon. (1989), and *Proceedings of the conference on forest resources crisis in the Third World 6–8 September 1986*, Sahabat Alam Malaysia, Penang, 1987.
293. Hart and Petrides in Lugo *et al.* (1987).
294. In a letter to the Institute of Current World Affairs.
295. In southwest Sumatra *Shorea javanica* has been planted in this way on 150–200 × $10^2$ ha, starting mid last century, (Torquebiau 1984) which makes them the largest agroforestry system of the humid tropics.
296. See various papers in McDermott (1988).
297. Wolf (1987).
298. Elliott (1988).
299. IUCN (1980).
300. Japan, USA, France, Germany, Holland, Ireland, Italy, Portugal, Spain, UK (Thomson in McDermott 1988). See also Secrett (1987).

301. Well-expressed in *Proceedings of the conference on forest resources crisis in the Third World 6–8 September, 1986*, Sahabat Alam Malaysia, Penang (1987), and evocatively in Waiko (1980).
302. Goodland and Irwin (1975).
303. Aiken and Leigh (1984) give an accessible summary.
304. *The Economist*, 6–12 August 1988.
305. Anon. (1985) and see the example of Costa Rica described by Gamez and Ugalde in Almeda and Pringle (1988).
306. Mr. S. Uno, National Diet of Japan, House of Councillors Foreign Relations Committee Meeting Record 4, 21 April 1988.
307. Gillis in Denslow and Padoch (1988) describes how timber from the west Malesian dipterocarp rain forests has been sold too cheaply.
308. Prescott Allen and Prescott Allen (1983).
309. See Bramwall *et al.* (1987).
310. Soulé and Wilcox (1980); Frankel and Soulé (1981); Soulé (1986, 1987).
311. Putz (1978). There are 130 virgin jungle reserves, of total area 106 500 ha.
312. Leighton and Leighton in Sutton *et al.* (1983); F. Lambert *ined*.
313. Caldecott (1988).
314. Kio (1978); Leslie (1987).
315. Evans (1982).
316. Sabah 43 000 ha planted, 200 000 ha planned; Peninsular Malaysia, 15 000 and 188 000 ha respectively (Salleh in McDermott 1988).
317. Yet ironically when a sena is felled in Singapore its timber goes to waste. Other fast-growing quality hardwood species that deserve fuller trial are *Acrocarpus fraxinifolius* of India and Burma, and *Cybistax donnell-smithii*, *Hibiscus elatus*, and *Tabebuia* spp. of tropical America. (L. J. Whitmore personal communication.)
318. D. U. U. Okali (personal communication).
319. Terborgh (1988).
320. Corlett (1988); 16 out of 30 mammals excluding bats, and 80 out of 150 bird species, have probably disappeared.
321. For example Stiles (in Almeda and Pringle 1988) has demonstrated that on the Caribbean slope of the mountains of Costa Rica 20–25 per cent of the rain forest birds migrate daily or seasonally from lowlands to highlands and can therefore only persist if forest is conserved at all elevations.

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# Glossary

When the reader encounters an unfamiliar word or concept he should first consult the index, because many of them are defined or described somewhere in the text. This glossary gives definitions of a number of specialized terms which it was not appropriate to cover in the main text. For standard scientific terms which are not familiar and which are not explicitly defined somewhere in the book the reader should consult a science dictionary. Two very useful ones are:

Allaby, M. (1985). *The Oxford dictionary of natural history*. Oxford University Press, Oxford.
Mabberley, D. J. (1987). *The plant book, a portable dictionary of the higher plants*. Cambridge University Press, Cambridge.

**albedo** The proportion of the incoming radiation that is reflected back from the Earth's surface; albedo varies for different wavelengths and types of land surface cover.

**alfisol** A relatively fertile tropical clay-rich soil, high in calcium and magnesium, of only limited occurrence (Table 8.1), well suited for agriculture.

**allopatry, allopatric** Refers to related species with different non-overlapping geographical areas of occurrence. See **sympatry.**

**Amerindian** The original inhabitants of the New World.

**andesite** A fine-grained volcanic rock which weathers to give a fertile soil.

**andosol** A fairly fertile soil produced by the initial weathering of volcanic ash; of very limited extent (Table 8.1).

**apomixis** Reproduction that does not involve the sexual process, with the consequence that the progeny have the same genetic constitution as their parents.

**aroid** A member of the family Araceae.

**association** A plant community with several or many co-dominant species. See **consociation**.

**autotroph** An organism that uses $CO_2$ as its main or sole source of carbon.

**basal area (BA)** The cross-sectional area of the trees of a block of forest (above a specified minimum diameter). BA is proportional to timber volume (BA × bole height) and so is a useful measure in forestry.

**biomass** The total weight of the living components of an ecosystem, usually expressed as dry weight per unit area.

**bromeliad** A member of the New World plant family Bromeliaceae which are mainly xeromorphic epiphytes.

**CAM** See crassulacean acid metabolism.

**canopy** Used here to mean the whole of a forest from the ground upwards. Some scientists use canopy to mean just the top of the forest, here called canopy top.

**cline** Gradual change across its distribution, without sharp disjunctions, of the gene frequencies or characters of a species.

**consociation** A plant community with a single dominant species. See **association**.

**coppice shoot** Shoot that arises from a bud at the base of a tree, usually one that has been cut down.

**crassulacean acid metabolism (CAM)** Special kind of metabolism which allow $CO_2$ to be absorbed at night when water loss is minimal and to be stored and used next day for photosynthesis. Common in Crassulaceae and other xerophytic succulent plants.

**cultivar** Cultivated variety, e.g. Malayan dwarf is a high-yielding, disease-resistant cultivar of coconut.

**dipterocarp** Member of the Dipterocarpaceae, pre-eminent tree family of lowland rain forests of western Malesia.

**diurnal** (daily) Applied to the rhythms found during a 24 hour night-day time period.

**diurnal range** The range expressed during the 24 hour night-day cycle.

**ecosystem** A community of plants and animals plus their physical environment.

**ectotrophic mycorrhiza (ectomycorrhiza)** A type of mycorrhiza in which the fungal hyphae do not penetrate the root cells but grow between them. Confined to rather few families of trees.

**emergent** A tree whose crown stands above the general level of the canopy top.

**endemism** Situation in which a species or other taxonomic group is confined to a particular geographic region which may be 'narrow', e.g. the beautiful ornamental tree *Maingaya malayana* is narrowly endemic to northwest Malaya, or 'wide', e.g. *Swietenia*, true mahogany, is a genus endemic to the neotropics.

**endotrophic mycorrhiza (endomycorrhiza)** Usually called vesicular arbuscular mycorrhiza; the fungal hyphae penetrate the root cells as little tree-like growths. Found in numerous plant families.

**eutrophic** Rich in nutrients. See **oligotrophic**.

**frugivore** A fruit eater.

**FAO** Food and Agricultural Organization (of the United Nations).

**folivore** A leaf eater.

**forest estate** The area of a nation set permanently aside for forestry; may include untouched forest, managed natural forest, and plantations, and be in public or private ownership or both.

**Glacial maximum** The height of an Ice Age when glaciation is at its maximum extent.

**greenhouse effect** Solar radiation which enters a greenhouse is reflected as long wavelengths which cannot pass through the glass, so the greenhouse heats up. Carbon dioxide, methane, oxides of nitrogen, and certain other gases in the lower atmosphere behave in the same way as glass. As these gases increase so does the amount of trapped solar energy, and this leads to climatic warming.

**hardwood** Wood of a flowering plant, technically recognized by its possession (with rare exceptions) of vessels. Hardwoods in fact range from hard and dense (e.g. Lignum vitae) to soft (e.g. balsa). See **softwood**.

**hemiparasitic** Plants that are partial parasites, able to fix $CO_2$ by photosynthesis but dependent on other plants for mineral nutrients. Sometimes misused with reference to stranglers (see text).

**heterotroph** An organism that uses organic carbon as its main or sole source of carbon.

**insectivore** An insect eater.

**kebun** (Malay garden) A term used in Indonesia and Malaysia for orchards and fields of mixed crops, home gardens.

**kunkar nodules** Nodules of concretionary calcium carbonate, formed within soil as a result of evaporation of mineral-rich water under a strongly seasonal or arid climate.

**leaf size spectrum** The division of leaves into a range of size classes (see Fig. 3.25), from leptophyll (very tiny) through nanophyll, microphyll, notophyll, mesophyll, and macrophyll to megaphyll (huge).

**lithology** The gross features of rocks.

**Malaya** The geographical region that encompasses the political states of Peninsular Malaysia and Singapore.

**Malesia** The phytogeographical region that stretches from the isthmus of Kra in south peninsular Thailand, throughout the Malay archipelago to the Bismarck archipelago northwest of New Guinea.

**Melanesia** The biogeographical region of the islands of the western Pacific Ocean, extending from the Solomon islands southwards to Vanuatu, New Caledonia, Fiji, Samoa, and Tonga.

**mesophyll** See leaf size spectrum.

**microphyll** See leaf size spectrum.

**monopodial** Tree crown with a single leading stem (leader), the branches lateral and often eventually falling off; commonly deep and narrow. See **sympodial**.

**monotypic** A genus that has only one species.

**mutualism** Interaction of two or more species that benefits both partners. See **symbiosis**.

**mycorrhiza** Close physical association between a fungus and the roots of a plant. See **endotrophic** and **ectotrophic mycorrhiza**.

**mymecophyte** Ant-plant.

**nanophyll** See leaf size spectrum.

**nectarivore** Nectar eating.

**neotropics** New World (American) tropics.

**niche** (ecological niche) The functional position of an organism in a community.

**notophyll** See leaf size spectrum.

**ochrea** A swollen enlarged ligule.

**OECD** Organization for Economic Co-operation and Development.

**oligotrophic** Poor in nutrients. See **eutrophic**.

**oxisol** An infertile loamy and clayey tropical soil,

of very wide occurrence (Table 8.1).

**palaeotropics** Old World tropics.

**pantropical** Throughout the tropics.

**PAR** Photosynthetically active radiation of wavelengths 400–700 nm, i.e. the visible spectrum. See Fig. 7.2.

**perhumid climate** A climate with no dry season.

**photophyte** A sun-loving plant commonly a xerophyte. See **skiophyte**.

**phytochrome** A photoreversible pigment found in plants which exists in two interchangeable forms, a red form in the presence of visible red light (660 nm) and a far-red form in the presence of far-red light (730 nm, beyond the visible spectrum). The amount of each form depends on the ratio of those two wavelengths in the light received by the plant.

**palynology** The study of pollen, and especially its use in the reconstruction of vegetation history.

**primary succession** The sequential change in vegetation commencing from the colonization of a new site.

**profile diagram** A conventional way of depicting the canopy of a forest, by a drawing of the trees larger than a specified small size on a long narrow strip, conventionally 60 × 6 m in size.

**radiocarbon dating** Atmospheric $CO_2$ contains a mixture of $^{12}C$ and the unstable radioactive isotope $^{14}C$ which has a half life of 5600 years. In dead plants the amount of $^{14}C$ progressively decreases, so the ratio of $^{14}C$ to $^{12}C$ can be used to measure the age of a piece of wood or other dead plant tissue.

**rattan** (Malay *rotan*) A climbing palm of subfamily Calamoideae. Rattans occur from Africa to Fiji and are abundant and economically very important in western Malesia.

**sclerophyll** A tough leathery leaf, in the humid tropics characteristic of heath forest.

**secondary succession** The sequential change in vegetation recolonizing a previously vegetated site.

**sere** The characteristic sequence of developmental stages occurring in primary or secondary succession (q.v.).

**skid trail** A foresters' term for the track in a forest along which logs are dragged or skidded. Sometimes called a snig track.

**skiophyte** A shade-loving plant. See **photophyte**.

**snig track** A foresters' term. See **skid trail**.

**softwood** Wood of a conifer, technically recognized by the absence of vessels. Softwoods have abundant fibres and make good paper. See **hardwood**.

**stand table** A foresters' term for the population of a tree species, usually divided into diameter or girth classes. See Fig. 7.11.

**sunflecks** Patches of direct sunlight which move across the floor of a forest.

**symbiosis** Said of species that live in close physical contact to their mutual benefit; a special kind of mutualism, q.v.

**sympatry** The occurrence of species together in the same area. See **allopatry**.

**sympodial** Tree crown with several main leading stems, commonly broader than deep. See **monopodial**.

**synusia** A life form community, e.g. big woody climbers.

**ultisol** An infertile loamy and clayey tropical soil, of very wide occurrence (Table 8.1).

**UNESCO** United Nations Educational Scientific and Cultural Organization.

**unit leaf rate (E)** The rate at which a plant gains dry weight per unit leaf area.

**xeromorphic** A plant with morphological and anatomical characters which appear adapted to withstand drought. See **xerophyte**.

**xerophyte** A plant that withstands drought.

# Index to plants and minor forest products

# General index

This book provides an introduction to the world's tropical rain forests for a broad readership, describing their structure and functioning, their value to man, and what he is doing to them. Examples are drawn from all parts of the humid tropics. Today there is more research being conducted in tropical rain forests than ever before. Some is driven by curiosity, some by desire to harness these forests to mankind's needs. What generalizations can be made? To what extent are there real differences between rain forests in different places, and what are the current frontiers of knowledge? Is present-day concern about man's impact on tropical rain forests justified? The author seeks to provide answers to these questions, in a form accessible to all who wish to know more about these luxuriant and diverse regions.

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